NEW FOSSIL PELOBATID FROGS AND A REVIEW OF THE GENUS *EOPELOBATES*

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CONTENTS

ABSTRACT

Eopelobates was a fossil pelobatid frog that lived in North America during the Eocene and early Oligocene, and may have been present in the Cretaceous as well. In Europe, it extended from middle Eocene through the middle Miocene. In many ways *Eopelobates* is intermediate between megophryine and pelobatine subfamilies, but is retained here in the Megophryinae because of absence of an enlarged prehallux, or spade. Two lines may be distinguished within the genus: a primitive, short-skulled group composed of the North American *E. guthriei* n. sp. and *E. grandis,* with the European *E. anthracinus* probably included here as well, and a long-skulled European lineage composed of *E. hinschei* (n. comb.) and *E. bayeri.*

The spadefoot toads were probably derived from *Eopelobates,* and the primitive *E. guthriei* shows some indications of spadefoot relationship. The earliest true spadefoot was *Scaphiopus skinneri* n. sp., from the early and middle Oligocene of North America. It has some primitive features but is already close to the modern *S. holbrooki.* A form close to *Pelobates* was also present in the early Oligocene of Europe, further implying at least an Eocene divergence of the spadefoots from the megophryines. The early or middle Oligocene *Macropelobates* from Mongolia links *Eopelobates* and the spadefoots in some

features, but the contemporaneous record of *Scaphiopus* described here indicates that it was too late to have been ancestral to the modern subfamily. *Macropelobates* is best interpreted as a relict of the spadefoot group that gave rise to both *Scaphiopus* and *Pelobates*. It seems to be most closely related to the primitive modern species *P. cultripes*, and also shows some similarity to the primitive *S. skinneri*. *Miopelobates*, a primitive pelobatine that lived in Europe in the middle Miocene and early Pliocene, may have been an early offshoot from the ancestral spadefoot.

The modern megophryines are tropical and subtropical and probably diverged from an *Eopelobates*-like form no later than the Cretaceous. *Leptobrachium* is the most primitive of the modern megophryines and is in some ways the most *Eopelobates*-like of the group. Megophryines of modern type were probably restricted to the southern part of the Eurasian continent during the early Cenozoic; they have undergone a separate radiation and have developed both high- and low-altitude terrestrial forms from the more aquatic, primitive types.

The Pelobatidae probably differentiated from a discoglossid-like ancestor in the Holarctic middle-latitude tropics, and the primitive aquatic megophryine *Eopelobates* gave rise to the terrestrial spadefoots in response to early Cenozoic climatic deterioration in both Europe and North America. Similarities between the two modern pelobatines indicate that they probably had a common ancestry.

INTRODUCTION AND ACKNOWLEDGMENTS

Although fossil frogs are relatively rare, the pelobatid frogs are one of the most frequently encountered frog families in the Cenozoic fossil record, especially in the Oligocene and Miocene. Many different forms have been described from North American late Cenozoic deposits and have

been recently reviewed by Kluge (1966) and Zweifel (1956). I am principally concerned here with the Eocene, Oligocene, and early Miocene forms and describe two new fossil finds that bear on the evolution of the Pelobatidae: (1) an early Eocene skull of *Eopelobates* from Wyoming, and (2) a skull and partial skeleton of a primitive *Scaphiopus* from the middle Oligocene of North Dakota.

Abbreviations

AM = American Museum of Natural History, New York City.

BM = British Museum (Natural History), London.

CUPI = Charles University Paleontological Institute, Prague.

FAM = Frick Laboratory, American Museum of Natural History, New York.

MCZ = Museum of Comparative Zoology, Harvard University, Cambridge.

MME = Museum für Mitteldeutsche Erdgeschichte, Geologisch-Paläontologisches Institut, Halle (Saale).

PU = Princeton University Museum of Geology, Princeton.

UCMP = University of California Museum of Paleontology, Berkeley.

UMMZ = University of Michigan Museum of Zoology, Ann Arbor.

THE STATUS OF THE GENUS EOPELOBATES

Eopelobates anthracinus Parker (1929) is from the lignite beds of Rott, near Bonn, Germany. It lacks a spade (Fig. 1) and is unlikely to have been fossorial. Parker called the beds Lower Miocene, but Westphal (1958) states them to be middle Oligocene (Rupelian). Špinar (1952) noted the presence of a larger, related species, *E. bayeri*, from Bechlejovice, near Děčin, Czechoslovakia, in beds of Chattian or Aquitanian age (late Oligocene or early Miocene). The presence of a spade was not determinable in his specimen. Hecht (1963, p. 23) suggested that *E. bayeri* was in fact referable to *Pelobates*. Zweifel (1956) referred a spadeless early Oligocene specimen from the Chadron Formation of South Dakota to a new species, *E. grandis*.

I have recently examined all published material of *Eopelobates* and have also had the privilege of studying both a new complete specimen of *E. bayeri* and an associated series of tadpoles of this species collected by Professor Špinar. He will describe these in detail but he has kindly allowed me to figure (Fig. 2) and briefly

discuss the adult animal in order to justify the generic assignment.

Except in a few cases in which the nature of the specimen precludes knowledge, material referred to *Eopelobates* shows the following features: (1) prominent, elongated sternal style; (2) strong posterior projection of the ischium; (3) spade absent; (4) long, relatively slender limbs; (5) urostyle either separate, partially, or completely fused with sacrum; (6) sacral diapophyses strongly dilated; (7) tibia longer than femur; (8) approximately subequal orbit and temporal openings; (9) dermal ossification well developed and fused to skull roof; (10) skull roof flat or concave dorsally; (11) ethmoid wide and blunt anteriorly, and with dorsal ethmoid roof over nasal capsules; (12) squamosal-frontoparietal connection absent; (13) prominent, well-ossified paroccipital processes on frontoparietal and occiput; (14) complete maxillary arcade; (15) femur-tibia length approaching or exceeding head-body length. Comparison with the two currently recognized subfamilies of pelobatids, the Pelobatinae and Megophryinae, indicates similarity of *Eopelobates* to both groups. The most clearcut megophryine resemblances are 2, 3, 4, 7, 8, 10, and 11. The only specific pelobatine feature is 9, but in a number of other features discussed below *Eopelobates* shows pelobatine resemblances. In 1, 6, 13, and 14 resemblance to both groups occurs. Character 5 is variable and useless as Zweifel (1956, p. 12) has suggested.

I believe that *in combination* characters 3, 7, 9, 10, 11, 12, and 15 validate *Eopelobates* as a distinct genus. In many ways, *Eopelobates* is intermediate between the two Recent subfamilies; this relationship will be discussed later in this paper. Zweifel's characterization of the genus (1956, p. 13) as extremely close to *Megophrys* is still valid, but it requires qualification. Hecht's contention (based only on the type) that *Eopelobates bayeri* is a

Figure 1.   *Eopelobates anthracinus*, BM R-4841; × 3

Pelobates is not supported by the new, complete specimen. There are indications, however, that an *Eopelobates*-like form gave rise to the spadefoot toads; these indications will be discussed below in the section on *Scaphiopus* and the new species of *Eopelobates* from Wyoming.

Following Zweifel (1956), a revised diagnosis of *Eopelobates* might read: pelobatid frogs with a fused encrustation

Figure 2. *Eopelobates bayeri*, CUPI 6.874; × 1. Left, 6.874a, imprint of ventral surface; right, 6.874b, counterpart, imprint of dorsal surface.

of dermal bone on the skull; skull roof concave or flattened medially; maxillary teeth present; eight procoelous presacral vertebrae; sacral diapophyses widely expanded; squamosal in wide contact with maxilla; no squamosal-frontoparietal contact; no bony prehallux or spade; tibia longer than femur; combined femur-tibiofibula length more than 90% of length from anterior tip of skull to tip of urostyle. This diagnosis differs from that of Zweifel in several respects. First, there is no frontoparietal-squamosal bar in *Eopelobates,* contrary to statements in the literature (see below under *E. grandis* and *E. anthracinus*). The term "postorbital bar" is confusing, since there is a possibility of "postorbital" contact both between maxilla and squamosal and between squamosal and frontoparietal. Neither Zweifel nor Parker were always specific in referring to this matter. Second, all species have a tibia either slightly or substantially longer than femur. Third, Zweifel (1956, p. 12) states that tibia and femur are "together somewhat shorter than the head-body length"; this is true of all Recent or fossil pelobatids measured by me, with the exception of *E. bayeri* and *E. hinschei* (see below).

The Family Assignment of Eopelobates

This has been discussed by Zweifel (1956). In the combination of procoelous vertebrae, imbricate neural arches, probable arciferal pectoral girdle, single coccygeal condyle, prominent sternal style, wide dilation of sacral diapophyses, long anterior and short posterior transverse processes, and the general aspect of the skull and skeleton, *Eopelobates* is referable to the Pelobatidae without much question.

Discussion of Anatomical Features

Before discussing the individual species of *Eopelobates,* a brief evaluation of selected anatomical features is necessary. Little or no attention will be given to features that have been treated adequately elsewhere or are not applicable to fossils.

Frontoparietal-Squamosal connection

Mertens (1923) believed *Pelobates fuscus* to be primitive because of the ligamentary frontoparietal-squamosal connection. Such a connection is not constant in either *P. cultripes* or *P. syriacus*. There is interpopulational variation as indicated by Başoğlu and Zaloğlu (1964; see also Fig. 27, this paper) and the connection may be absent in small individuals of *P. cultripes* (MCZ 15376). In most Recent megophryines, except *Leptobrachium hasselti* and *Scutiger mammatus*, a specialized connection of frontoparietal and squamosal occurs on the surface of the prootic, ventral to the temporal musculature (Fig. 11d).

Absence of the superficial, sculptured frontoparietal-squamosal connection in both *Eopelobates* and the Oligocene pelobatine *Macropelobates* probably indicates the primitive pelobatine condition. I believe, however, that Gislén (1936) was correct in suggesting that *Pelobates cultripes* is primitive, although my reasons for this decision are different from his (see section below on *Pelobates*).

In *Megophrys,* dermal ossification spans frontoparietal and squamosal, and Zweifel (1956, p. 15) has suggested that the presence of considerable dermal bone may be a primitive condition. While it is true that a complete bony head casque may develop in large individuals of *Megophrys carinensis, M. monticola,* and perhaps other species, this is not fused to the skull bones, but instead coalesces from peculiar, irregular dermal plaques that usually remain separate, even though they grow to meet each other. Dermal covering lacks discrete boundaries and may extend into the skin of the dorsum; it is therefore quite different from the sculptured, fused, and discrete ossifications of pelobatines and *Eopelobates*. Whether it is an independently derived condition or a degeneration from a fused, *Eopelobates*-like condition cannot be determined. Many fossil frogs have

secondary dermal sculpture on the skull roof, and these forms occur as far back as the late Jurassic; some other Jurassic frogs, however, lack dermal sculpture. Extensive dermal skull sculpture is present in some Hylidae, Leptodactylidae, Ranidae, Bufonidae, Rhacophoridae, and Discoglossidae; most of these groups have acquired this dermal covering independently.

Prootic Foramen

Kluge (1966, p. 13) has shown some apparent morphogenetic trends in the shape of the prootic foramen (= trigeminal foramen). There is a tendency for this to be surrounded by bone in some species, but in general, the foramen is open anteriorly (e.g. in *Megophrys* and in *Pelobates cultripes*). The foramen is narrow in both *Scaphiopus* (*Scaphiopus*) and the one species of *Eopelobates* in which this is known (*E. guthriei* n. sp.; see p. 309). In *Pelobates fuscus,* this foramen is elongated vertically and in some specimens may be surrounded by bone, as in *Scaphiopus* (*Spea*).

While a trend toward closure does seem to exist, this is quite variable throughout the pelobatid series, as might be imagined in a condition involving minor degrees of ossification. The actual shape variation is even greater within species than Kluge indicated (Fig. 16). Care should be taken in the use of this character. Study of the soft structures involved would be useful, as would a functional study of the correlation of closure of foramen with the loss of dermal roofing bone.

Orbitotemporal Opening

The proportions of orbit and temporal opening vary widely in pelobatids (Fig. 15). In *Megophrys* and *Eopelobates,* the skull is relatively broad and flat and the orbito-temporal openings are of about equal size. In pelobatines there is a tendency towards the enlargement of the orbit and the reduction of the temporal area and

rear part of skull. This is most extreme in *Scaphiopus couchi* and S. (*Spea*), and results in a major change in the squamosal angle (see below and Figs. 15, 17). Other skull changes accompany this one and result in the high, domed, toad-like skull of these species.

Squamosal Angle

Griffiths (1963, p. 248) gave three categories for the condition of the angle between squamosal and quadratojugal, and for the origin of the depressor mandibulae: (1) depressor mandibulae originating from the squamosal stem and otic arm; squamosal angle > than 55° (Bufonidae, Brachycephalidae); (2) muscle originating from squamosal and dorsal fascia, squamosal angle 45°–50° (Ranidae, Microhylidae, Rhacophoridae, Leptodactylidae, Hylidae); (3) muscle originating only from dorsal fascia, squamosal angle < 45° (Discoglossidae, Pelobatidae). He noted that all groups passed through condition (1) in their development and that care should be taken in using this character because of the possibility of parallel paedomorphy.

In specimens I measured, the squamosal angle was 45° or less only in *Megophrys;* but in *Eopelobates guthriei* nov. (see below), *E. hinschei,* and *Scaphiopus skinneri* nov. (see below), the angle fell between 45° and 50°. All other pelobatines were between 56° and 73°, the highest in S. *couchi.* This change in the squamosal angle suggests that the development of a higher skull and larger orbit in pelobatines (discussed above) may involve a paedomorphic trend.

Ossified Sternum

Kluge (1966, p. 17) noted that Griffiths (1963, p. 271) was incorrect in stating that all pelobatids have an ossified sternal apparatus. Zweifel (1956, p. 24) states that the sternum is cartilaginous in *Scaphiopus.* This seems to be true in general, but a specimen of S. *couchi* chosen at random
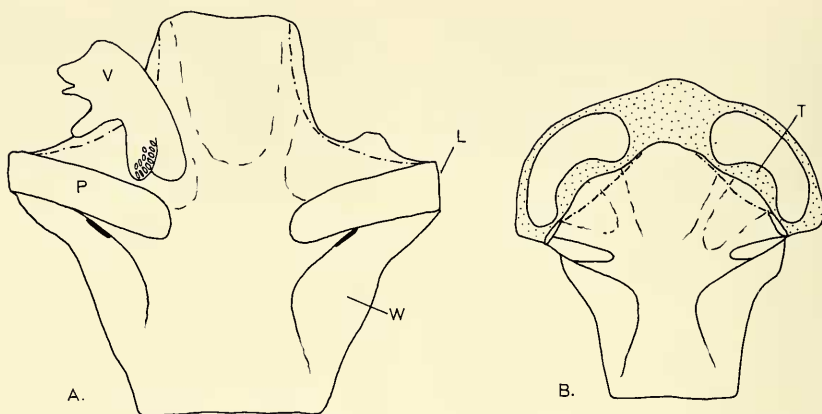
Figure 3. (A) *Megophrys carinensis,* AM 23965, ventral view of ethmoid and vomer; (B) *Megophrys robusta,* MCZ 25735, ventral view of ethmoid, ethmoid cartilage stippled; both × 3. — . — . — . — . — = dorsal border of ethmoid roof; L = lateral process; P = palatine articulation surface; T = turbinal fold in cartilage; V = vomer; W = lateral wing.

(MCZ 64374, cleared and stained) has an irregular sternal ossification (Fig. 9d) in the stylar region, and an ossified, paired omosternum as well. Although this condition has not yet been described in a fossil *Scaphiopus* and I have not checked it in *S. holbrooki,* it is possible that some ossification is the primitive condition in *Scaphiopus.*

Ethmoid

The ethmoid shows considerable intergeneric variation in general shape, and since it is often found in fossils it can be useful in identification. I lack sufficient material for a meaningful study on intrageneric variation, but the material available seems to be relatively consistent and to demonstrate that some species may be identifiable on this basis as well.

In *Megophrys* the ethmoid is pinched-in ventrally, but develops lateral wings dorsally, giving a rhombic shape to the dorsal surface of the bone. In *Leptobrachium* no lateral wings are present and the ethmoid is hour-glass shaped. The lateral processes (Fig. 3) are prominent, but are not strongly separated from the anterior process by emargination in the choanal region. The

palatines underlie the lateral processes and the vomers lie along the lateral sides of the anterior process. Internally there is only a faint development of a turbinal fold between lateral and anterior processes, if it is present at all (Fig. 4); however, a turbinal fold is present in cartilage. The internal surface is flattened dorsoventrally and the capsule area is completely roofed by the ethmoid; only at the anterior end is it covered by the nasal. In *Pelobates cultripes* and *P. syriacus,* the anterior process is moderately developed, but the end of the process is relatively blunt with only a slight median projection. The turbinal fold is moderately developed.

In *Pelobates fuscus* and especially in *Scaphiopus,* there is marked separation of the anterior and lateral processes by emargination. In the emarginated area between those processes, *P. fuscus* has a moderately developed turbinal fold, and *Scaphiopus* a very well developed one. In both species (except *S. holbrooki*), the turbinal fold projects strongly in ventral view as the capsular process (Fig. 5), and the anterior process itself has two separate projections. The capsular process is much better developed in *Scaphiopus* (again,
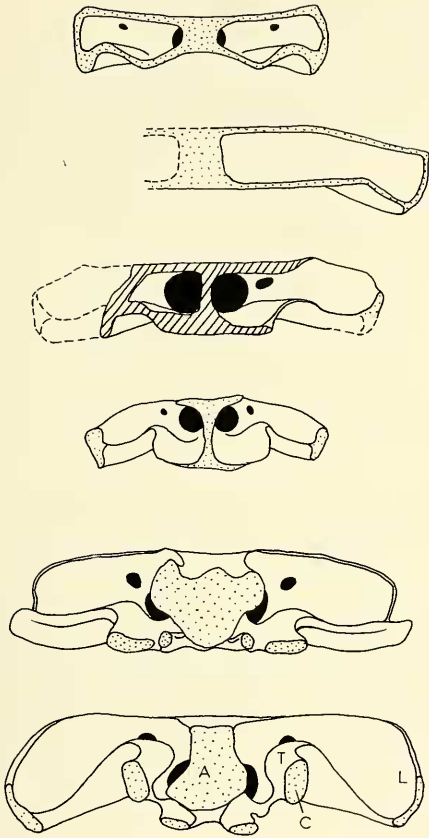
Figure 4. Ethmoids in anterior view; a, *Megophrys monticola*, AM 23964; b, *Eopelobates grandis*, PU 16441; c, *Macropelobates osborni*, AM 6252; d, *Pelobates cultripes*, UMMZ S-2630; e, *Pelobates fuscus*, MCZ 1012; f, *Scaphiopus couchi*, AM 56284; a–d, × 3; e–f, × 6; diagonal hatching = broken surface, dashed line = restoration, stippled area = cartilage attachment surface; A = anterior process; C = capsular process; L = lateral process; T = turbinal fold.
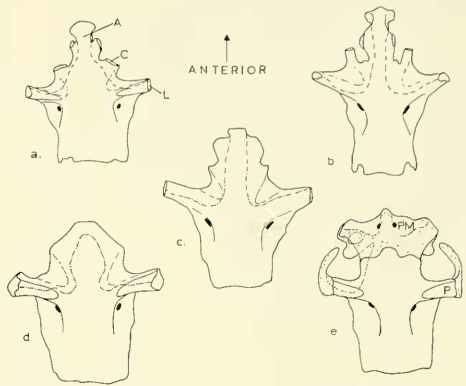

Figure 5. Pelobatine ethmoids in ventral view; a, *Pelobates fuscus*, MCZ 1012; b, *Scaphiopus couchi*, AMNH 56284; c, *S. holbrooki*, MCZ 25577; d, *P. cultripes*, UMMZ S-2730; e, *P. varaldii*, MCZ 31970, with ethmoid cartilage in stipple; all × 2. Irregular line = depression; — . — . — . — . — = dorsal border of bony ethmoid; __ __ . __ __ . __ __ = dorsal border of ethmoid cartilage. A = anterior process; C = capsular process; L = lateral process; P = palatine articulation surface; PM = premaxillary articulating surface.

except in *S. holbrooki*) and is somewhat different than in *Pelobates fuscus*.

In *Eopelobates* intermediate conditions prevail, so far as this can be determined in the fossil material. There is definite separation of lateral and anterior processes by emargination in *E. bayeri*, although the general configuration is more *Megophrys*-like than pelobatine. The anterior process as shown in *E. guthriei* n. sp. and *E. bayeri* ossifies very little (see p. 312 and Fig. 6), and remains broad as in megophryines.

This situation is approached in *P. varaldii* (separated from *P. cultripes* by Pasteur and Bons, 1959; Fig. 5e, this paper). A separate anterior process is not present on *E. grandis* (Fig. 7) and is not visible in the other species. In the ventral view of *E. bayeri*, a depression develops between lateral and anterior processes, reflecting a weak turbinal fold development like that of *Megophrys* and *Pelobates*, but not as distinct as in *Scaphiopus*. The ethmoid of *Macropelobates* is as in *P. cultripes*, as far as can be determined (cf. Figs. 7b; 5d).

In all pelobatines, the dorsal ethmoid roof of the nasal capsule is absent and the entire capsule is then roofed by the nasal (Fig. 5), but in *Megophrys* the ethmoid floor and roof are of about equal extent and the nasal provides cover for the capsules only anteriorly (Fig. 7). The extent of roofing by ethmoid in *Eopelobates* can be seen only in *E. grandis*, and is approximately as in the megophryines. In the subgenus *Spea* of *Scaphiopus*, the anterior process may become extremely large and
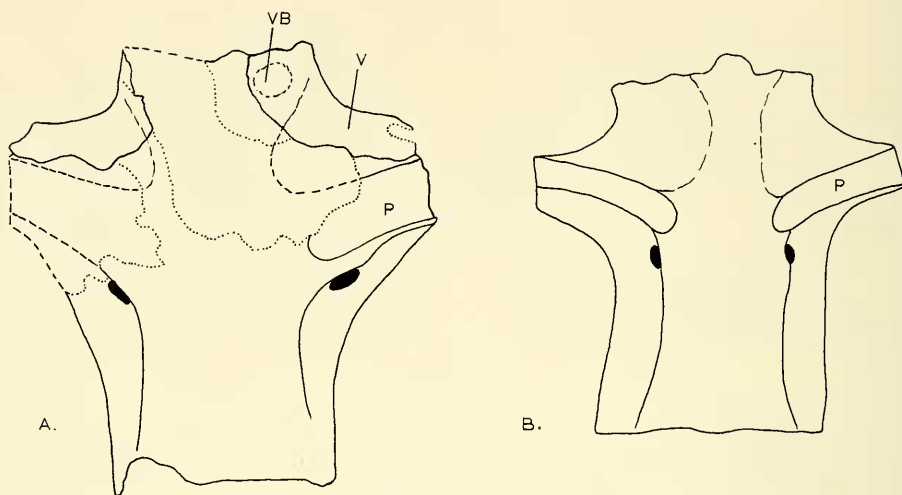
Figure 6. Ventral view of ethmoid of (A) *Eopelobates guthriei*, MCZ 3493, × 3; (B) *E. bayeri*, CUPI 6.874, × 5.5. Dashed line = restoration, dotted line = broken bone outline; P = palatine articulation; VB = boss for vomerine teeth.

flared anteriorly (e.g. *S. intermontanus*), producing the most extreme pelobatine condition.

The bony ethmoid is, of course, merely an ossified portion of the ethmoid cartilage and not coextensive with it. The cartilage itself is also quite different in the two modern subfamilies (cf. Figs. 3b, 5e) and within that cartilage, the above-noted variations in ossification occur. The retreat of the bony roof of the pelobatine ethmoid is accompanied by regression of the cartilage to a partial ring surrounding the naris and a thin, membranous cover over the main unossified part of the capsule.
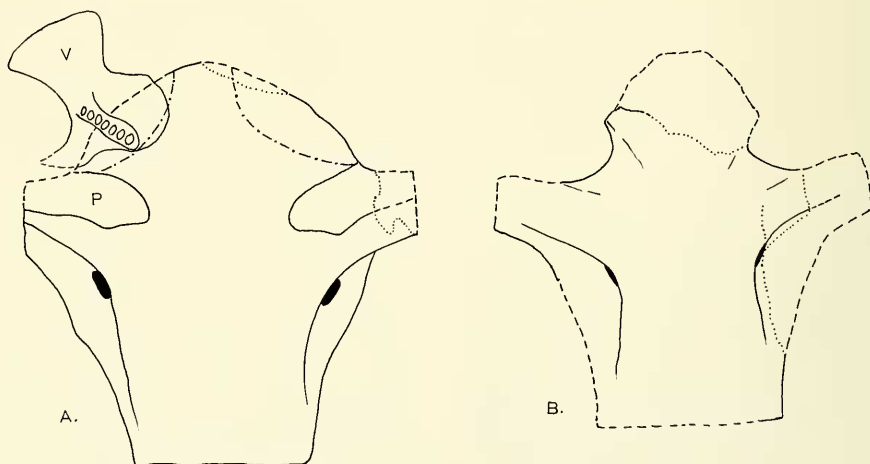
Figure 7. (A) *Eopelobates grandis*, PU 16441, ventral view of ethmoid and vomer; (B) *Macropelobates osborni*, AM 6252, ventral view of ethmoid; both × 3. Dashed line = restoration; dotted line = broken bone surface; _ . _ . _ . _ = dorsal border of ethmoid; V = vomer; P = palatine articulation surface.
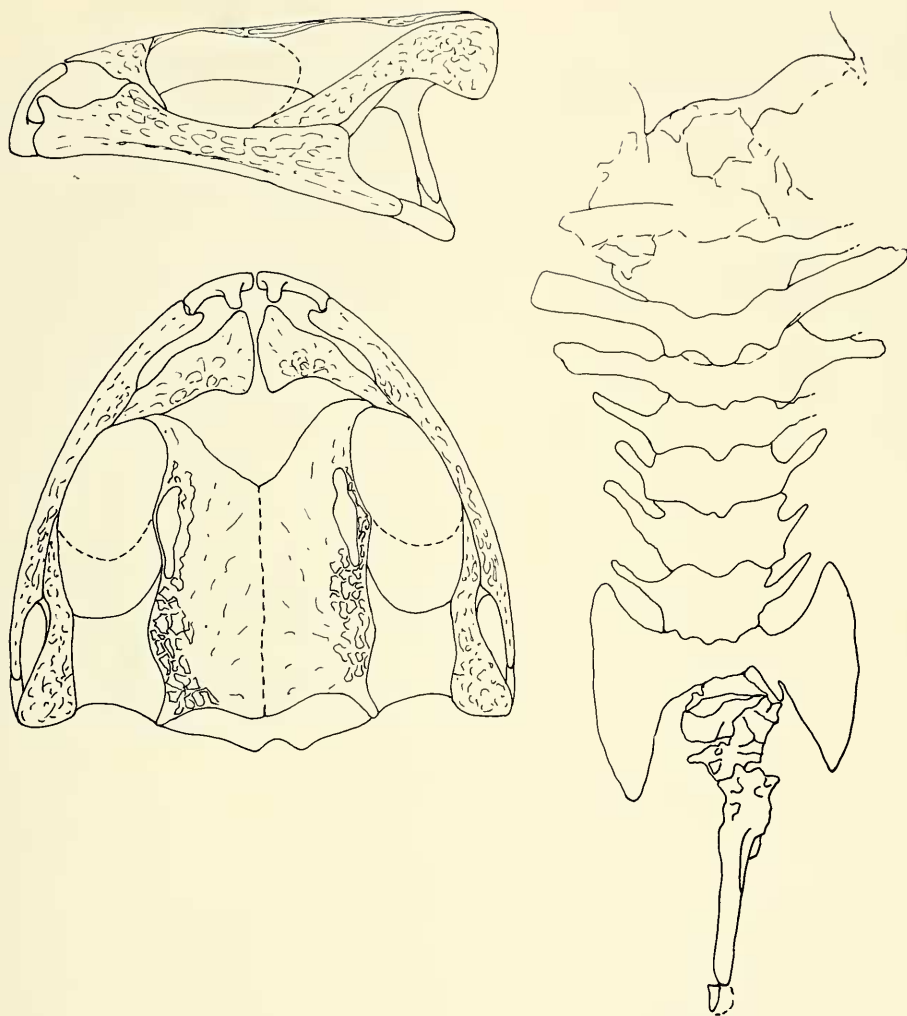
Figure 8. *Eopelobates anthracinus*, type, BM R-4841; left, restoration of dorsal and lateral views of skull; right, camera lucida drawing of vertebral column, posterior skull roof outline shown anteriorly; × 6.

Without the knowledge that the large rodlike anterior process is present in cartilage in *Pelobates cultripes*, the similarities of *Pelobates fuscus* and *Scaphiopus* in ethmoid construction might seem to indicate that the spadefoot genera are closely related through *P. fuscus*, but the latter is not likely to be ancestral to the North American spadefoots, as is discussed further below. *Scaphiopus holbrooki*, the most primitive member of the genus, is intermediate between *P. cultripes* (or *P. syriacus*) and other *Scaphiopus* in this regard; *S. couchi*, *S.* (*Spea*), and *P. fuscus* have independently ossified the anterior process of the ethmoid as far anteriorly as the premaxillae.

It would be of considerable interest to study olfaction within the pelobatines; their nasal capsules indicate some strong adaptive trends not seen in the aquatic *Megophrys* and *Eopelobates*.
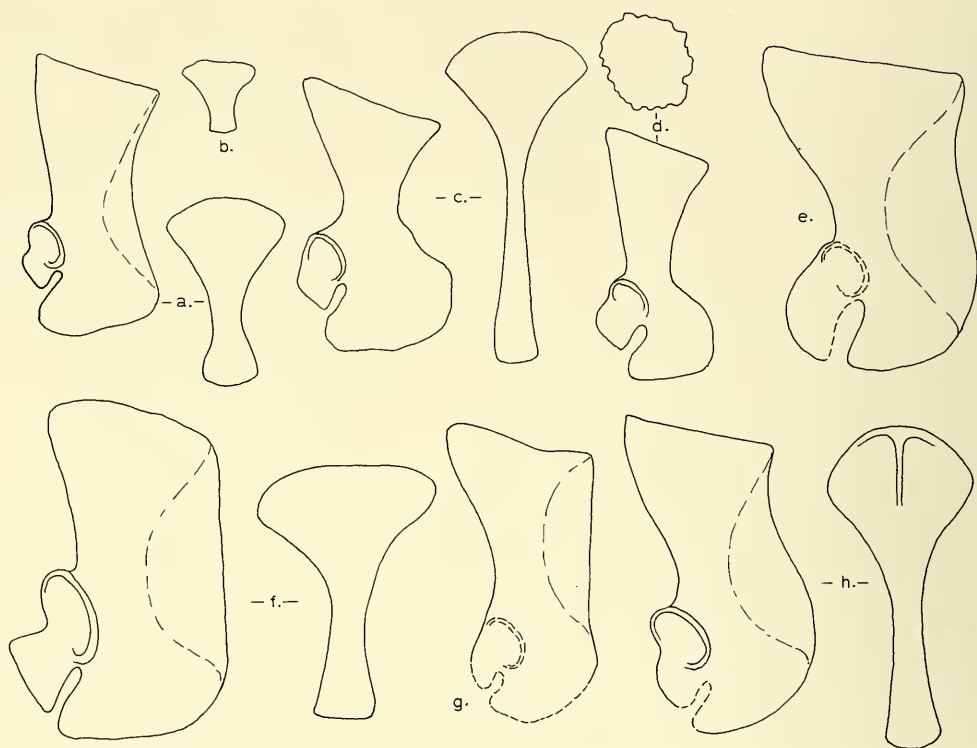
Figure 9. Scapulae and sternal styles of pelobotids. a, *Pelobates cultripes*, UMMZ S-2629; b, *P. syriacus balcanicus*, MCZ 50690, style only; c, *Megophrys monticola*, AM 23964; d, *Scaphiopus couchi*, MCZ 64374; e, *Eopelobates hinschei*, MME 6692, scapula only; f, *E. grandis*, PU 16441; g, *E. anthracinus*, BM R-4841, scapula only; h, *E. bayeri*, CUPI 6.874; a–g, × 3; h, × 4.5.

Chronological Review of Described Eopelobates

CLASS AMPHIBIA
SUPERORDER LISSAMPHIBIA
ORDER SALIENTIA
Family Pelobatidae

Eopelobates anthracinus Parker 1929

Parker's account is good, but better knowledge of other species allows some additional discussion. In the skull, the pattern is approximately as Parker described it, but contrary to the implication of his figure, there is no process of the squamosal leading towards the frontoparietal; this is partly the result of the bone being underlain by the pterygoid and partly the result

of crushing in the area. Also, the squamosal is more hatchet-shaped posteriorly than in his figure. The frontoparietal shows prominent, well-defined pits on the lateral edges, and sculpture is more apparent laterally than medially. Because of crushing, the exact shape of the frontoparietal is difficult to determine, but it is about as indicated in Figure 8. There is a groove between the two halves of the frontoparietal that probably indicates a suture, but since all adult *E. bayeri* specimens appear fused, this cannot be certain. There is a complete maxillary arcade; the quadratojugal can be seen clearly on the photograph (Fig. 1), and there is a strong quadratojugal process of the maxilla. The teeth are pedicellate. The bone in the left orbit that

Figure 10. *Eopelobates hinschei*, MME 6692; × 3; see Table 1, 8a.

Parker thought was the dentary is actually the prearticular. The anterior tip of the parasphenoid appears to be visible near the anterior end of the left frontoparietal, but the impression is vague. In the postcranial skeleton, imprints of transverse processes on all vertebrae occur on the matrix, contrary to Parker's statement: these are long on the anterior vertebrae but short and anteriorly directed on the posterior ones (Fig. 8) in accord with other species of *Eopelobates*, *Pelobates*, and some *Megophrys*. Again contrary to Parker, the cleithrum is visible on the morphological left side.

Parker remarks (1929, p. 280) that the skull "appears to have been almost identical with that of the recent *Pelobates*." In fact, the skull differs from that of *Pelobates* and *Scaphiopus* and resembles that of other *Eopelobates* in having a flattened or concave skull table and in having approximately subequal orbit and temporal openings. The dermal sculpture is coarse and open, more or less as in the other European *Eopelobates*.

There is an anterior lamina on the scapula (Fig. 9). The urostyle is separate and there were two, perhaps three, postsacral vertebrae, although crushing makes the exact number uncertain (Fig. 8).

The skull restoration of *Eopelobates anthracinus* (Fig. 8) was made from camera lucida tracings of the individual bones; the tracings were then fitted together. Since the bones were all flattened after burial, their somewhat different shape in the restoration results from curvature incorporated into the three dimensional
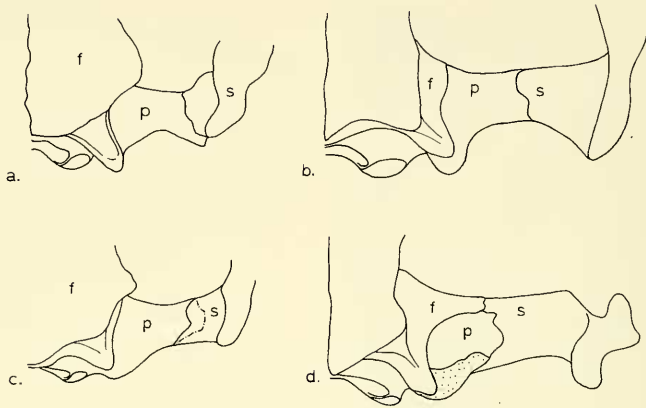
Figure 11.   Right posterior half of pelobatid skulls, dorsal view. a, *Scaphiopus h. holbrooki*, MCZ 58003; b, *Eopelobates guthriei*, MCZ 3493; c, *Pelobates fuscus*, MCZ 1012; d, *Megophrys lateralis*, AM 23549; all × 3. f = frontoparietal; p = prootic; s = squamosal; _ . _ . _ . _ . _ = margin of prootic covered by squamosal; cartilage stippled.

model. The skull height (especially anteriorly) is the major feature in doubt, but as given it is approximately intermediate between the flattened skulls of *Megophrys* and the domed skulls of *Pelobates* and *Scaphiopus*. The bone outlines do not allow much deviation either way from the outline suggested here. There is a well-defined groove between the frontoparietals, but a distinct suture cannot be seen. The exact shape and placement of the nasals is conjectural, but the arrangement given is consistent with what remains of the bones. The photograph of the specimen (Fig. 1) does not allow confirmation of all bone outlines; this was only made possible by comparing many photographs taken with light coming from different angles and from drawings made at the time of study of the original specimen.

Eopelobates hinschei (Kuhn, 1941)

This species was originally described as *Halleobatrachus hinschei* by Kuhn (1941, p. 353) from the middle Eocene Geiseltal deposits near Halle, Germany. As Špinar (1967, p. 218) correctly pointed out, this species belongs to the Pelobatidae rather than to the Palaeobatrachidae. Much of the other material described by Kuhn also belongs to the genus *Eopelobates*. All the characters of the genus are clearly visible in this series of specimens. The photograph given here (Fig. 10) shows one of the best skulls available. Kuhn gave six generic and seven specific names to this sample, but on the basis of proportions alone, the fossils can easily be related and demonstrated as a growth series (Fig. 25). Hecht (1963, p. 23) has already commented accurately on the reliability of Kuhn's study, but contrary to Hecht, however, Špinar (1967) has shown the presence of palaeobatrachids at Geiseltal.

I think it unlikely that *Eopelobates bayeri* (Špinar, 1952) is conspecific with *E. hinschei*. As Figures 19 and 20 show, the squamosals are different, and there are proportional differences of the nasals. However, the two species are related and both have rather elongated frontoparietals, though that of *E. bayeri* is fused (Fig. 12). Their scapulae are also similar (Fig. 9e, h), as is their ratio of tibiofibula-femur to head-vertebral column length (Fig. 29). Prof. Špinar is presently studying the specimens of *E. hinschei* and *E. bayeri*, and his report will deal with this matter more fully.

Table I lists the synonymy of *Eopelobates hinschei* as I interpret the Geiseltal remains.
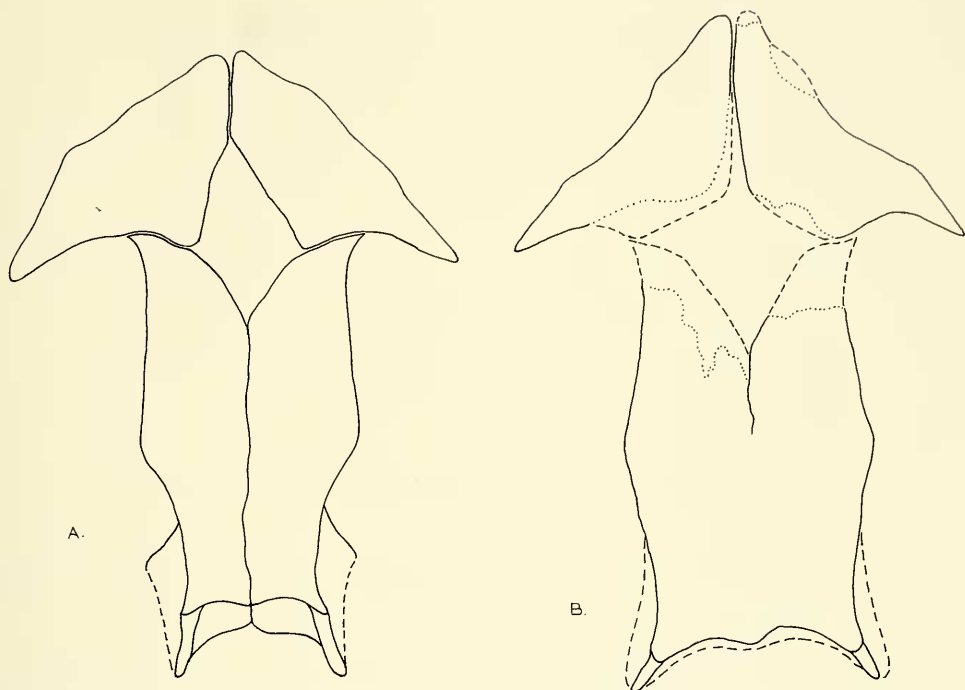
Figure 12. Skull roof of (A) *Eopelobates hinschei,* MME 6692 (8a, Table 1), ✕ 4.5; (B) *E. bayeri,* CUPI 6.874; ✕ 4.8; dashed line = restoration; dotted line = broken bone outline.

Eopelobates bayeri Špinar 1952

As the figure shows, the late Oligocene —middle Miocene Czechoslovakian species *E. bayeri* has all of the characters of the genus noted above (Figs. 2, 12b). Variation may exist with respect to fusion of urostyle and sacrum; in the type specimen of *E. bayeri,* they appear to be separate (perhaps because of poor preservation), but in the new complete specimen are apparently fused. They are separate in *E. bayeri* tadpoles as in tadpoles generally. *E. bayeri* has a somewhat similar squamosal to *E. anthracinus,* but other features, such as frontoparietal shape and ratio of limb to body (Fig. 29), are different. Both species have more sculpture laterally than medially on the frontoparietal, but *E. bayeri* lacks the large pits seen in *E. anthracinus.* The two species seem quite clearly different. The Czechoslovakian

material confirms the absence of a spade, and the orientation and shape of the transverse processes is in accord with those of the other specimens of *Eopelobates,* some *Megophrys,* and *Macropelobates.*

Of special interest is the shape of the ethmoid, which is well shown on the new specimen of *Eopelobates bayeri* (cf. Figs. 2, 6). It is similar to that of *E. guthriei* n. sp. (see p. 312) but differs from that of *E. grandis.*

The exact contour of the nasals is conjectural. They have been thrust backward over the frontoparietals, and their relations to the latter in the restoration have been determined by triangulation with other skull parts and by comparison with other *Eopelobates* specimens (including the type of *E. bayeri*). On the left side of the restoration (morphological right; the specimen is an imprint), the two parts of the

nasal thrust apart by crushing have been rejoined. Compensation for flattening of the nasals in preservation has been made laterally in the restoration in order to make all restorations comparable.

Eopelobates neudorfensis (Wettstein-Westersheimb, 1955) was based on disarticulated elements derived from a Middle Miocene (Helvetian) fissure filling in southern Czechoslovakia. Most of the diagnostic elements are preserved. The frontoparietal is fused except at the anterior margin and is indistinguishable from that of the new specimen of *Eopelobates bayeri*. The squamosal has a hatchet-shaped tympanic process as in *E. bayeri* and *E. anthracinus* (Fig. 19c). The maxilla has a strong posterior process for the quadratojugal. Urostyle and sacrum are separate. The close association of this species with *E. bayeri* in morphology, time, and geography indicates that it is a synonym of the latter.

Eopelobates grandis Zweifel 1956

A few additions and corrections can be made to Zweifel's excellent account of this early Oligocene North American species (Zweifel, 1956). Although the maxilla and squamosal are in firm contact, there is *no* contact of squamosal and frontoparietal as Zweifel indicated (1956, p. 5). The right squamosal, on which he apparently based this interpretation, has been rotated and displaced up against the frontoparietal. Normal relationships to the frontoparietal are retained by the left squamosal, as confirmed by *Eopelobates anthracinus*, *E. bayeri*, and *E. guthriei* n. sp. (see p. 311). The squamosal shape is more rounded than Zweifel's figure indicates, and is essentially a deeper version of the *E. guthriei* squamosal (*cf*. Figs. 19d and 20d). The frontoparietal differs from that of *E. guthriei* and *E. anthracinus*, but, except for being relatively short, it is in accord with that of other *Eopelobates* (Fig. 13a).

The quadratojugal (identified as stapes by

Zweifel) is present and is excavated for a posterior projection of the maxilla as in *Megophrys*. The vomer is now exposed (Fig. 7a) and is like that of *Pelobates* in having a rather expanded anterior wing, an almost transversely-oriented tooth row (rather than a patch), and a dorsal flange clasping the side of the ethmoid as in *P. cultripes*. The ethmoid is more megophryine than in any other *Eopelobates*. It is flattened and dilated anteriorly, and has prominent lateral processes that are deeply notched on their ventral surfaces for the palatines (Fig. 7a). The dorsal surface of the ethmoid is little emarginated. The order of difference from ethmoids of other *Eopelobates* is about the same as between those of the modern species *Megophrys carinensis* and *M. robusta* (Fig. 3). The scapula has a well-developed anterior lamina (Fig. 9f), which has a straight anterior border as in *E. anthracinus*.

The wide posterior extent of the nasal resembles that of *E. guthriei* n. sp. (see Fig. 13) and the pelobatines. This resemblance tends to link the two American species, but I believe it unnecessary to distinguish them generically. Zweifel's reference of this species to *Eopelobates* is undoubtedly correct; it is probably a distinct species because of ethmoid shape, wide frontoparietal, and rounded tympanic process of the squamosal. Hecht (1963, p. 23) has suggested that this animal is a distinct genus, but it differs no more from other *Eopelobates* than the Recent *Megophrys carinensis* differs from *M. lateralis*, for instance.

Eopelobates sp.

Hecht (1959, p. 131) described a megophryine sacrum from the middle Eocene Tabernacle Butte local fauna of Wyoming and correctly noted a close resemblance to *Eopelobates grandis* Zweifel. It is reasonable to refer the Tabernacle Butte specimen (AMNH 3832) to *Eopelobates* without specific designation.
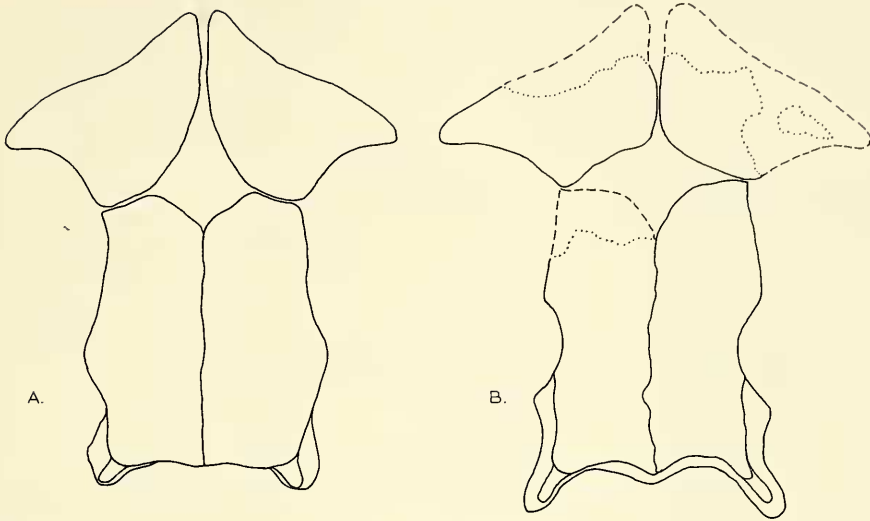
Figure 13. Skull roof of (A) *Eopelobates grandis*, PU 16441, ✕ 1.8; (B) *E. guthriei*, MCZ 3493, ✕ 3. Dashed line =
restoration; dotted line = broken bone outline.

Młynarski referred to *Eopelobates* sp. material from the Pliocene of Poland. The specimens consist only of sacra having separate urostyles. Other fused sacra and urostyles and characteristic skull elements he referred to *Pelobates* cf. *fuscus*. Since, however, *Eopelobates* is otherwise unknown later than middle Miocene, and since *Pelobates cultripes* often has partially or completely separated urostyles, it seems unlikely that *Eopelobates* is represented in the Polish material, at least in the absence of characteristic skull elements. These elements may be referable to *Miopelobates* (see below). Since the salamander *Andrias* is now known to occur in the European Pliocene (Westphal, 1967) there is no apparent reason why *Eopelobates* might not also have persisted, but at present there is insufficient reason to confirm its extension beyond the middle Miocene.

DESCRIPTION OF NEW MATERIAL OF
  EOPELOBATES

Eopelobates guthriei, n. sp.

Type: MCZ 3493, nearly complete skull and associated fragmentary scapula.

Diagnosis: Differs from other species of *Eopelobates* in having a narrow tympanic process of the squamosal combined with a triple emargination of the frontoparietal margins and a relatively short skull.

Etymology: Patronym for Dr. Daniel Guthrie, who collected the unique specimen in 1962.

Locality: NE 1/4, SE 1/4, Sect. 16, T 39 N, R 90 W, Fremont County, Wyoming.

Horizon: Upper part of the Lysite member, Wind River Formation.

Age: Early Eocene (Lysitean, late Sparnacian equivalent).

Preservation: Only the skull, portions of the prearticular region of the jaws, and an associated fragment of left scapula are present (Fig. 14). The slightly crushed skull is well preserved on the right side, but on the left the temporal region is missing. The premaxillae, the anterior portions of the nasals, and the anterior part of both maxillae are missing.

Although the skull is slightly flattened, distortion is limited for the most part to the peripheral tooth-bearing and temporal bones. The ventral borders of the maxillae

Figure 14. *Eopelobates guthriei,* n. sp.; holotype skull, MCZ 3493; *a,* right lateral, *b,* occipital, *c,* dorsal, and *d,* ventral views; early Eocene, Wyoming; × 2; coarse stipple = matrix.

are warped laterally, a condition especially true of the left maxilla, whose lateral aspect now faces almost dorsally. Ventrally, the left palatine has been pushed dorsally away from the ethmoid, but it seems to have retained its natural relationship to the latter.

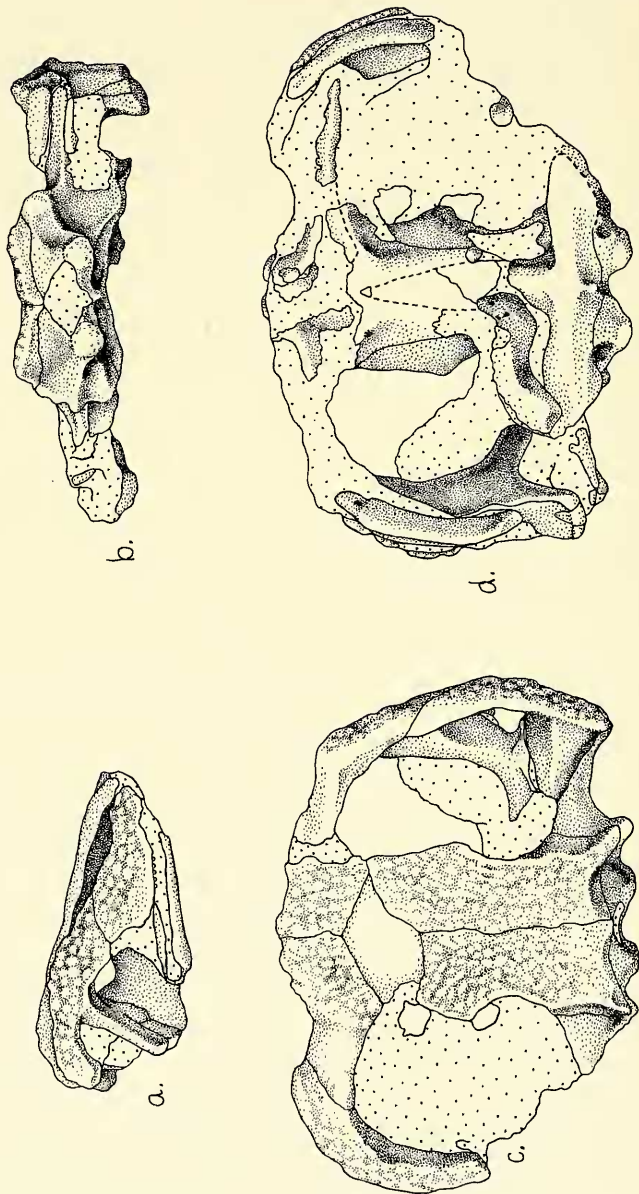*Description*: The skull indicates a rather broad-headed animal with subequal dorsal temporal excavations and orbits, separated by postorbital processes. The dorsal skull region is flattened and concave medially and bounded by weak crests. The skull as a whole is covered with a well-developed dermal sculpture.

Posteriorly the nasals meet on the midline, diverge at their posterior borders to expose the ethmoid, barely meet the frontoparietals, and extend laterally to meet the maxillae. The nasals are weakly crested in the area continuous with the lateral borders or the frontoparietals, and slope toward the midline between these crests. The nasals are sculptured on their entire preserved surface.

Located between the frontoparietals and the nasals is a smooth, somewhat diamond-shaped portion of the ethmoid, which is the center of a depression bounded anteriorly by the nasal crests mentioned above and posteriorly by the lateral borders of the frontoparietals. The depression extends to the posterior border of the skull.

The paired frontoparietals are subrectangular in shape and prominently sculptured. The postorbital processes are situated anteriorly about two-thirds the frontoparietal length from the apex of the foramen magnum. The anterior tip of the left frontoparietal is missing, increasing the apparent depth of the ethmoid depression. The anterior tip of the right frontoparietal touches the nasal at its lateral border. The undistorted occiput, the lateral crests of the frontoparietals, and the symmetry of the cranial roof indicate that the midline depression of the frontoparietal, ethmoid, and nasals is natural. The postorbital processes are the widest points on the frontoparietals

except for the posterior tips, which extend onto the paired projections of the paroccipital processes on the occiput dorsal to the condyles. Posteriorly the frontoparietal reaches the apex of the foramen magnum, from which point lambdoidal crests form concave curves, extending towards the paired projections noted above.

In occipital view the median skull roof is depressed; the highest points are on its lateral borders. The occipital surface of the skull is well preserved and relatively little distorted; there is little breakage except for the missing left temporal region. The most prominent bones are the otoccipitals, which meet above and below the triangular foramen magnum. The large circular foramina for the ninth and tenth cranial nerves are recessed at the base of the prominent hemispherical occipital condyles. Lateral to these foramina, the otoccipital forms the posterior border of the fenestra ovalis, forming a prominent rounded process underlain by the parasphenoid. Laterally the otoccipital forms a prominent knobbed paroccipital process, which is capped by the frontoparietal. The stapes is forked proximally and is closely appressed to the ventral surface of the lateral extension of the otoccipital. The fenestra ovalis is open ventral to the proximal end of the stapes and dorsal to the rounded process of the otoccipital mentioned above; a large opercular space is present as in recent spadefoots, and since the very delicate stapes is preserved in place, a calcified operculum was probably absent.

The right squamosal has been displaced dorsally at its posterior articulation with the otoccipital; in fact it has pivoted somewhat (along with pterygoid and maxilla) on the lateral tip of the otoccipital, so that the greatest dorsal displacement is at the medial end of the squamosal, and the descending (quadrate) process of the squamosal has been rotated mediad, carrying with it the remains of the lower jaw. The quadrate is represented by a small sliver

clasped between squamosal and pterygoid. The posterior end of the lower jaw is missing, as are the tip of the quadrate and the posterior border of the maxilla; apparently the quadratojugal and posterior process of maxilla (if present) were broken off in the dislocation of the temporal region.

In the ventral view, the posterior portion of the parasphenoid is well preserved, but the cultriform process is faulted by the right scapula and then terminates by breakage at the ethmoid border. The parasphenoid extends anteriorly from the border of the foramen magnum to the posterior border of the ethmoid. The lateral arms of the parasphenoid form the floor of the fenestra ovalis region. Prominent nuchal, pterygoid, and retractor bulbi muscle scars, set off a trapezoidal, flattened area midway between the lateral arms of the parasphenoid.

The otoccipitals extend posteriorly somewhat beyond the posterior borders of the parasphenoid, completing the fenestra ovalis region ventrally.

There is a large opening in the posterior braincase region, bounded anteriorly by ethmoid, ventrally by parasphenoid, posteriorly by otoccipital, and dorsally by frontoparietal. The major cranial nerves emerged through this opening, but only the prootic foramen has any individuality. It is a narrow suboval notch, open anteriorly.

The ethmoid is broadly exposed between the parasphenoid and the vomers, and ventral processes of the frontoparietals clasp it laterodorsally. It sends broad, crested processes laterally toward the maxillary arcades, and posterodorsal to each of these open the foramina for the anterior (orbital) extensions of branches of the occipital arteries. Anterior to each lateral ethmoid process is a depression, from which bone is missing as a result of erosion and breakage. Anterior to these depressions, the curved choanal borders of the vomers are still preserved in natural position. A raised area over the left an-

TABLE 2

MEASUREMENTS OF *EOPELOBATES GUTHRIEI*

The following measurements (in mm) are relatively unaffected by crushing or distortion:

1. posterior median height of the skull from the most dorsal point on the frontoparietals to the most ventral point on the midline of the parasphenoid 4.9
2. height of foramen magnum 2.0
3. width of foramen magnum 4.0
4. maximum width across the paroccipital processes 11.1
5. maximum width across occipital condyles 6.2
6. maximum length of stapes as preserved 4.7
7. maximum length of frontoparietal from apex of foramen magnum to anterolateral tip 12.0
8. length from apex of foramen magnum to postorbital process 8.3
9. maximum anteroposterior length of right squamosal 11.2
10. length of posterior projection of squamosal behind anterior margin of tympanic cavity 5.0
11. maximum width across postorbital processes of frontoparietals 9.0
12. maximum height of posterior process of squamosal 2.0

terior part of the ethmoid probably represents the left vomerine tooth plate. The other parts of the vomers are not preserved. Laterally, an irregular, broken bar of bone seen on the left side probably represents the palatine.

The pterygoid is present as a complete bone only on the right side, and is strongly curved, bending broadly toward the quadrate region on the one hand, and toward the otoccipital and maxilla on the other.

In lateral view the relationships of the maxilla, squamosal, quadrate, pterygoid, and prearticular are undistorted on the right side. On the left side, only the middle part of the maxilla is present; the temporal region and premaxilla are missing.

The maxillae bear pedicellate teeth and are heavily sculptured in a pattern similar to that of the frontoparietals. On the right side, the posterodorsal corner of the maxilla meets the squamosal in a broad horizontal suture.
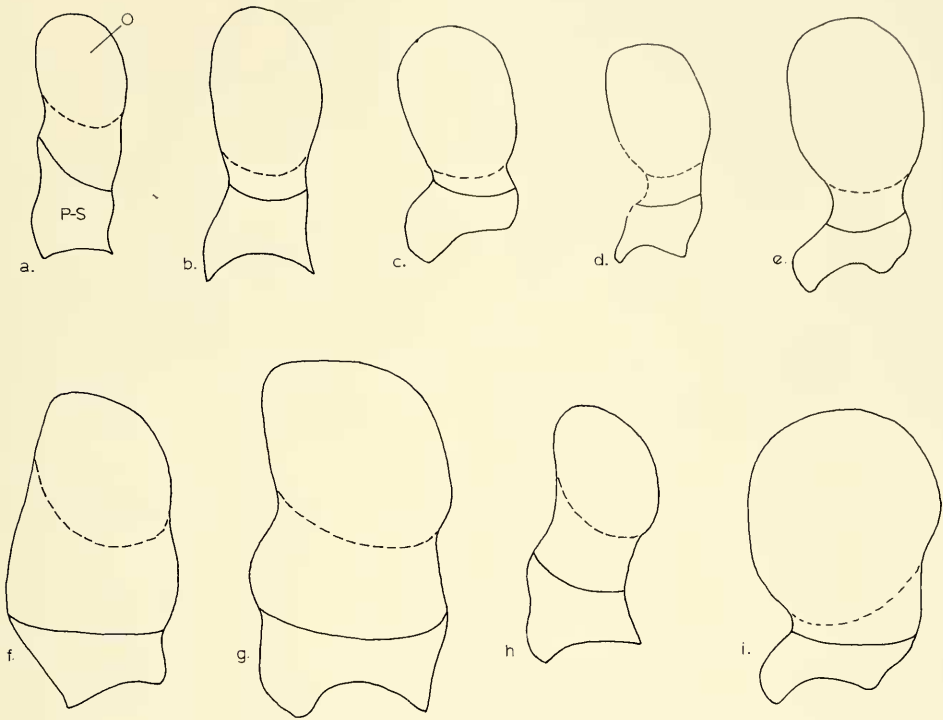
Figure 15. Orbitotemporal opening relationships in pelobatids; all are of right side, anterior towards the top. a, *Eopelo-bates anthracinus*, BM R-4841; b, *E. grandis*, PU 16441; c, *Pelobates fuscus*, MCZ 1012; d, *Scaphiopus skinneri*, FAM 42920; e, *S. holbrooki*, MCZ 58003; f, *Megophrys carinensis*, AM 23965; g, *E. hinschei*, MME 6692; h, *E. guthriei*, MCZ 3493; i, *S. couchi*, AM 14478. Not to same scale; O = orbit; P–S = prootic and squamosal roof of ear region; dashed line = posterior border of orbit in all, and restored portion of frontoparietal in d.

The T-shaped squamosal is well preserved on the right, and, like the maxilla, is sculptured on the crossbar of the T. Anteriorly the bone is much broader than it is posteriorly. The posterior process of the squamosal curves posteriorly over the tympanic cavity, expands slightly at its posterior border, and forms an acute angle with the descending process of the squamosal. The latter process is flattened anteroposteriorly and has a sharp crest separating the tympanic cavity from the lower temporal excavation. The descending process is closely applied to the posterolateral border of the pterygoid, and is separated from it ventrally by the sliver of quadrate noted in the description of the occipital view. The ventral portion of the quadrate is lost, as is the articular. Pieces of the prearticulars indicate the position of the lower jaws, and lie in their natural positions ventromedial to the maxillae.

The crushed and fragmentary left scapula has been rotated 180° and now lies on the right side. Its posterior border is broken and little, if any anterior lamina appears to have been present.

Discussion: Because of the possession of a concave skull roof, approximately subequal orbital and temporal openings, and the distinctive shape of squamosal and ethmoid (Figs. 14, 13b, 19, and 20), reference of this specimen to *Eopelobates* seems clear.

In the proportions of nasals and frontoparietals, *E. guthriei* shows the relatively short skull characteristic of pelobatines and *E. grandis*, whereas the European

species, except for *E. anthracinus,* are more elongated and megophryine in these characters. *E. anthracinus* also shows the triple frontoparietal emargination of *E. guthriei,* but in squamosal shape there is close agreement between *E. guthriei* and the middle Eocene *E. hinschei* from the Geiseltal. In both of the latter, the anterior maxillary process of the squamosal is more expanded than the tympanic process, which is narrow and forms a wide, laterally visible roof to this part of the tympanic cavity. This roof lacks dermal sculpture (Fig. 20b, d, R). In dorsal view, *E. guthriei* resembles *Scaphiopus* and *E. grandis* in the excavation of the posterior border of the otoccipital and squamosal (Fig. 15).

The ethmoid of *E. guthriei* is incomplete and poorly preserved anteriorly but seems to resemble that of *E. bayeri* and (so far as can be seen in the crushed material) *E. hinschei;* it is relatively shorter as a result of the less elongate skull of the American form. The vomer has a broad, flat process on the posterior border of the choana as in *Leptobrachium hasselti,* the most primitive megophryine (Inger, 1966, p. 21) rather than a short, pointed process as in *Megophrys. E. grandis* has a similar process to *E. guthriei,* but it is relatively smaller and closer to the *Megophrys* condition.

The occiput of *E. guthriei* is quite pelobatine in its well-ossified paroccipital processes and tubera, its general proportions and relatively simple stapes. Unfortunately, the occiput is not known in any other specimen of *Eopelobates.*

Comparison of Figures 12, 13, and 17–23 shows that, in combination, squamosal and frontoparietal shape distinguish the modern pelobatid species. Since the specific status of the latter is based on many other criteria not available in fossils, these characters can be confidently applied to fossil samples. Either character separately may be useful, but wherever possible the two should be used together.

By this criterion the separate species
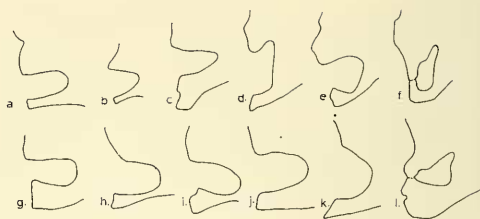
Figure 16. Anterior parts of left prootic bones showing prootic foramina. a, *Megophrys carinensis,* AM 23965; b, *M. monticola,* AM 23964; c, *Eopelobates guthriei,* MCZ 3493; d, *Pelobates fuscus,* MCZ 1012; e, the same, MCZ 1353; f, the same, right side (reversed); g, *Scaphiopus h. holbrooki,* MCZ 58003; h, *S. skinneri,* FAM 42920; i, *S. h. hurteri,* AM 44244; j, *S. couchi,* AM 57642; k, *S. couchi,* AM 14478; l, *S. intermontanus,* AM 16916. a–b, × 2; c–l, × 4.

status of *E. guthriei* and the Gieseltal *E. hinschei* is shown by their different frontoparietal proportions. Their squamosals are very similar and show Eocene transatlantic similarities, a phenomenon already observed in many fossil mammals and lizards. Yet there are minor proportional differences between the squamosals of the two Eocene species that are of the order of magnitude seen in modern species such as *Scaphiopus holbrooki* and *S. couchi.*

The frontoparietals of *Eopelobates guthriei,* however, are relatively shorter than in either *E. hinschei* or *E. bayeri,* and are very similar to those of *E. grandis* and *E. anthracinus* (cf. Figs. 8, 12, 13). The general proportions of the posterior end of the skull are more as in megophryines than as in pelobatines (Fig. 11); the posterior border of the prootic part of the otoccipital, however, is expanded posteriorly as in *Scaphiopus* (and to a lesser degree in *Megophrys*) but not as in *Pelobates,* in which the tip of the prootic is narrow as in *Macropelobates* (Fig. 11). Unfortunately, this condition is not known in other *Eopelobates.* The prootic foramen of *E. guthriei* (Fig. 16) resembles that of *Megophrys carinensis* and most *Scaphiopus* (*Scaphiopus*) in its rather elongate, simple, and unrestricted opening; there is no approach to the restricted or closed opening seen in *Pelobates* and *S.* (*Spea*).
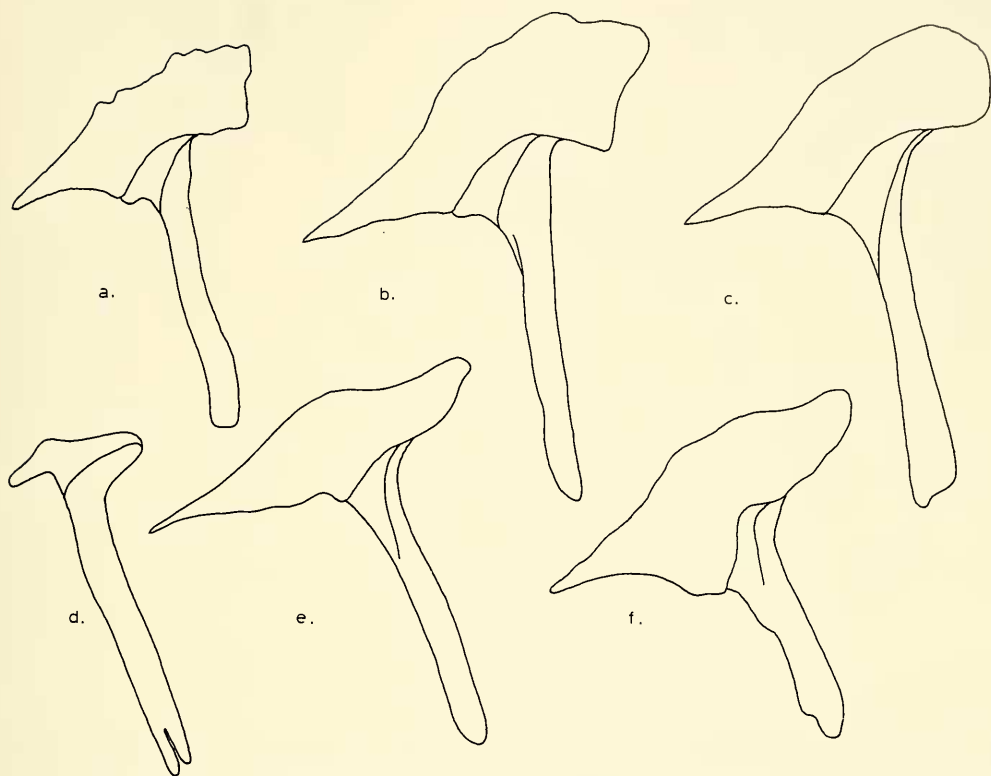
Figure 17. Left squamosals of pelobatids. a, *Scaphiopus couchi*, AM 56284; b, the same, AM 57641; c, the same, AM 14478; d, *S. intermontanus*, AM 16916; e, *S. holbrooki hurteri*, AM 44244; f, *S. h. holbrooki*, MCZ 58003; all × 6.

?*Eopelobates* sp.

In 1964, I described disarticulated and questionably pelobatid remains from the late Cretaceous Lance Formation of Wyoming. These elements included humeri, ilia, a urostyle, and a maxilla. The ilia (Estes, 1964, fig. 31c) closely resemble those of most pelobatids and the superior acetabular expansion is relatively small as in *Pelobates cultripes, Macropelobates,* some *Eopelobates,* and the discoglossids. The urostyle is megophryine in possessing a single articular cotyle and transverse processes; discoglossid and ascaphid urostyles also have the latter but have a double condyle as well.

The squamosal cited as hylid-like (Estes, 1964, fig. 31a-b) closely resembles that of *Eopelobates guthriei* and *E. hinschei* and is probably pelobatid rather than hylid. In 1964, I recognized resemblances of this squamosal to those of pelobatids (p. 60), but lacking knowledge of Eocene *Eopelobates,* I was reluctant to refer a squamosal of such unusual shape to the Pelobatidae. The maxilla (Estes, 1964, fig. 31d-e) lacks sculpture and may not be referable to the pelobatids. A fragment of a maxilla that has sculpture like that of the squamosal is now known (AMNH 8133, V5620, Lance Formation, Wyoming). The nasal questionably referred to the Hylidae (Estes, 1964, p. 60) may also be pelobatid on the basis of sculpture similarity to the other specimens.

It is possible that the Lance Formation specimens may be an early record of either *Eopelobates* or of a related pelobatid per-
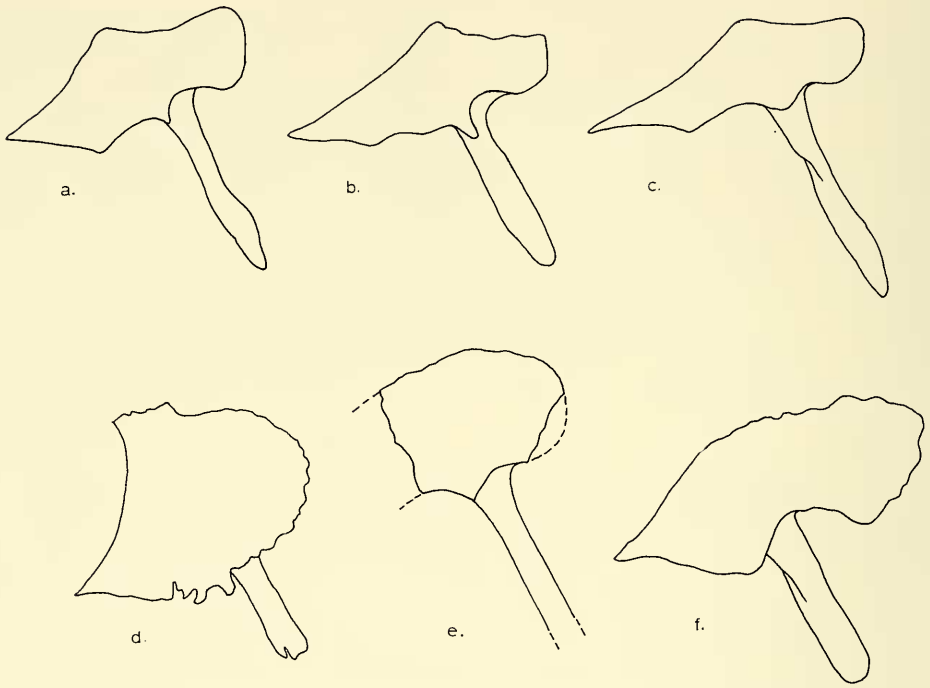
Figure 18.   Left squamosals of pelobatids. a, *Pelobates fuscus*, MCZ 1353; b, the same, MCZ 1013; c, the same, MCZ 1012; d, *P. cultripes*, UMMZ S-2630; e, *Macropelobates osborni*, AM 6252; f, *Scaphiopus skinneri*, FAM 42920.   Dashed line = restoration; a–c, × 6; d–f, × 3.

haps nearer to the discoglossids. Unfortunately, without articulated or at least more extensive material the reference must remain tentative. New material from the Lance Formation and from other late Cretaceous localities has made the association of the remains somewhat more assured now than in 1964. Several discoglossids are present in these localities (Estes, 1969) and are represented by well-preserved and distinctive skeletal elements different from those considered here.

THE RELATIONSHIPS OF EOPELOBATES

In his original discussion, Parker (1929, p. 280) suggested that *Eopelobates anthracinus* was a late representative of Noble's (1924, p. 9) "first stage" of pelobatid evolution, one in which ribs, an acromion, reduction of pubis, and expansion of sacral diapophyses were found. Parker also noted

a close similarity in the proportions of *E. anthracinus* to those of *Macropelobates*. The latter genus exemplified Noble's "second stage" of pelobatid development by development of prehallux, dermal skull casque, and further expansion of the sacral diapophyses. In 1952, Špinar made more explicit the relationship of *Eopelobates* to *Megophrys* in his discussion of a second species of *Eopelobates*. Zweifel (1956), in describing a third species, *E. grandis*, suggested that *Eopelobates* might be included as a subgenus of *Megophrys*, but that such a course would involve "investigation of other units within *Megophrys* probably worthy of subgeneric rank." The description here of a new Eocene species of *Eopelobates*, the recognition of the excellent series of *Eopelobates* specimens (here referred to as *E. hinschei*) from the Geiseltal middle Eocene, and the new
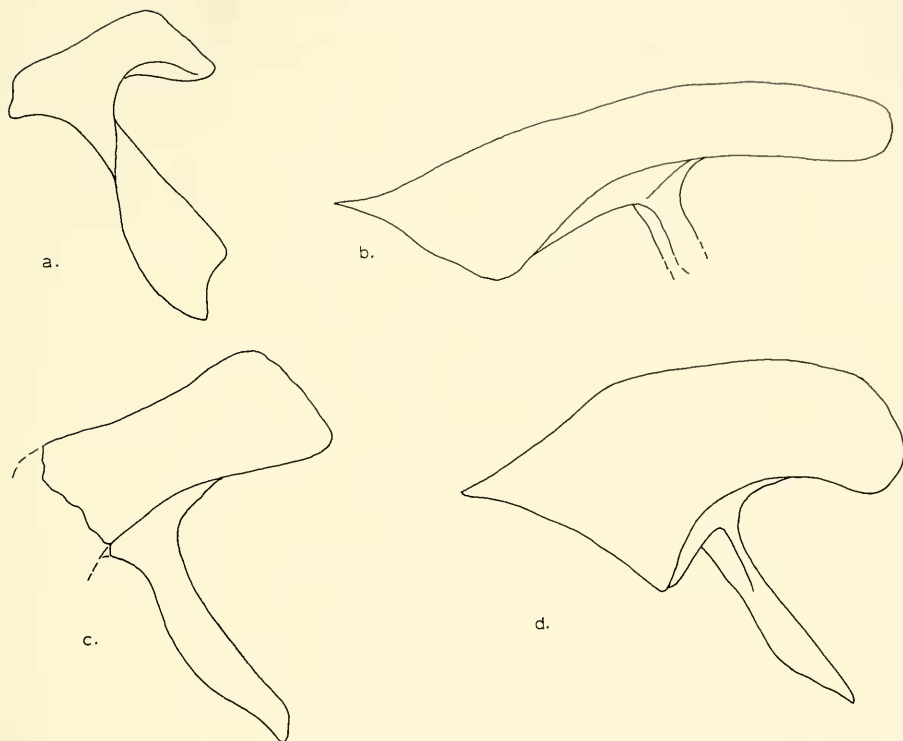
Figure 19. Left squamosals of pelobatids. a, *Megophrys lateralis*, AM 23549; b, ?*Eopelobates* sp., UCMP 44707; c, *E.* "*neudorfensis*" (= *bayeri*); d, *E. grandis*, PU 16441. Dashed line = restoration; a–b, × 6; c, × 10; d, × 3.

specimen of *E. bayeri* make it possible now to take a closer look at the relationships of *Eopelobates*. Redefinition of *Macropelobates* has also been necessary, and this will be discussed below.

Eopelobates was a relatively widespread and common early and middle Cenozoic frog first known with certainty from early Eocene of North America and middle Eocene of Europe. These two forms, *E. guthriei* and *E. hinschei*, respectively, show relationship to each other in their squamosal shape, although *E. hinschei* has already developed the long skull table seen later in *E. bayeri*. The relationship between the two Eocene forms is probably real, however, and demonstrates another similarity in early and middle Eocene continental transatlantic vertebrate faunas (Simpson, 1947). This similarity first ap-

pears in the late Paleocene mammalian and lower vertebrate faunas (Russell, 1964; Estes, Hecht, and Hoffstetter, 1966). Yet the time difference and the differentiation into long and short-headed forms indicate that the intercontinental similarity is not so specific as to imply direct connection.

It is possible, as noted above, that *Eopelobates* (or an ancestor) was already present in the late Cretaceous of North America. Relevant material is very fragmentary, however, and the record must be used with care.

Eopelobates does not recur in Europe until the middle Oligocene of Germany, when *E. anthracinus* indicates the presence of the short-headed lineage. The long-headed line begun by *E. hinschei* in the Eocene leads directly to the late Oligocene
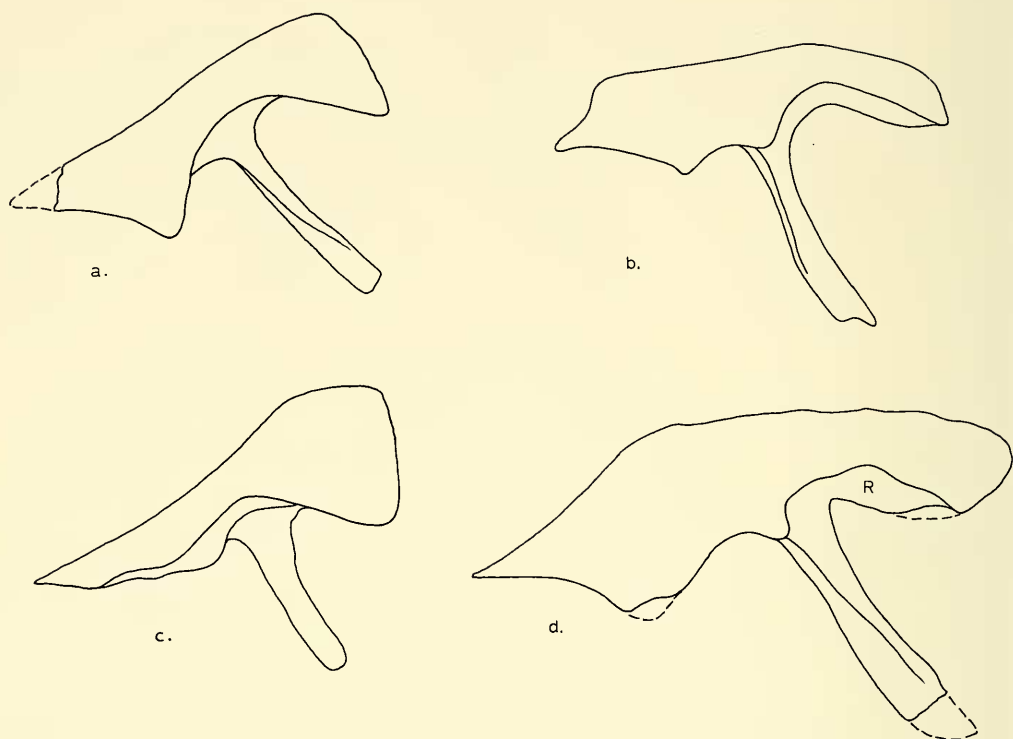
Figure 20.   Left squomosols of pelobotids.   a, *Eopelobotes bayeri,* CUPI 6.874; b, *E. hinschei,* MME 6753; c. *E. onthracinus,* BM R-4841; d, *E. guthriei,* MCZ 3493.   Dotted line = restorotion; a, d, × 6; b, × 5; c, × 9.5.
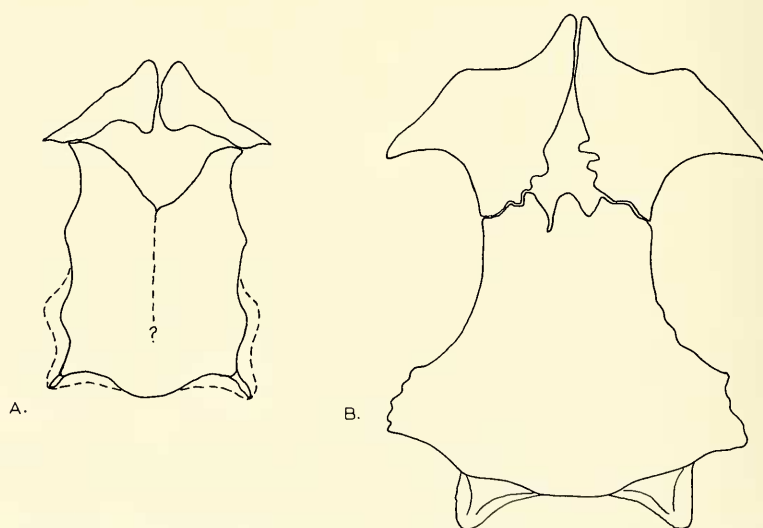
Figure 21.   Skull roof of (A) *Eopelobotes onthracinus,* BM R-4841, obout × 10; (B) *Pelobates cultripes,* UMMZ S-2631, × 3; doshed line restored.
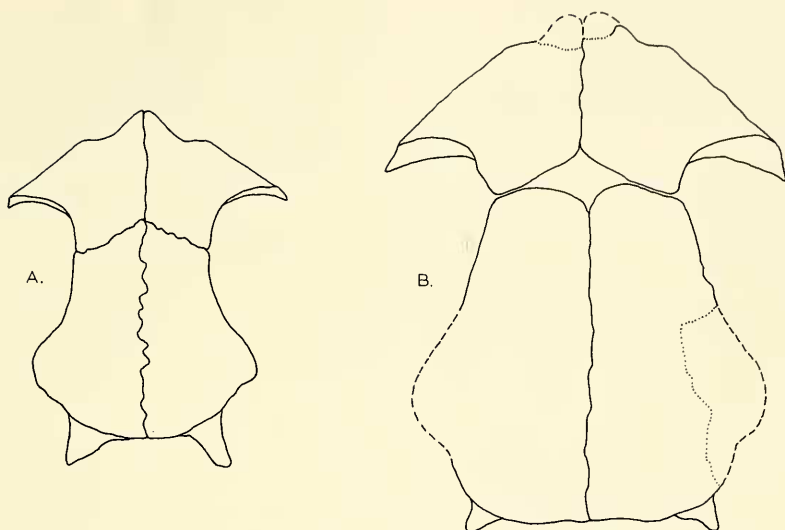
Figure 22. Skull roof of (A) *Scaphiopus h. holbrooki*, MCZ 58003; (B) *S. skinneri*, FAM 42920; both × 3. Dashed line = restoration; dotted line = broken bone outline.

(or early Miocene) and middle Miocene *E. bayeri* from Czechoslovakia. In North America, *E. grandis* continues the short-headed line into the early Oligocene but then apparently becomes extinct.

Eopelobates is characterized by a number of features listed at the beginning of this paper, the most distinctive being gen- erally long-limbed proportions, absence of dermal head casque fused to the skull. The body proportions differ from those of most megophryines in having a greater relative elongation of the vertebral column and urostyle as well as a lengthening of limb segments, especially the tibiofibula, which is significantly longer than the femur. In
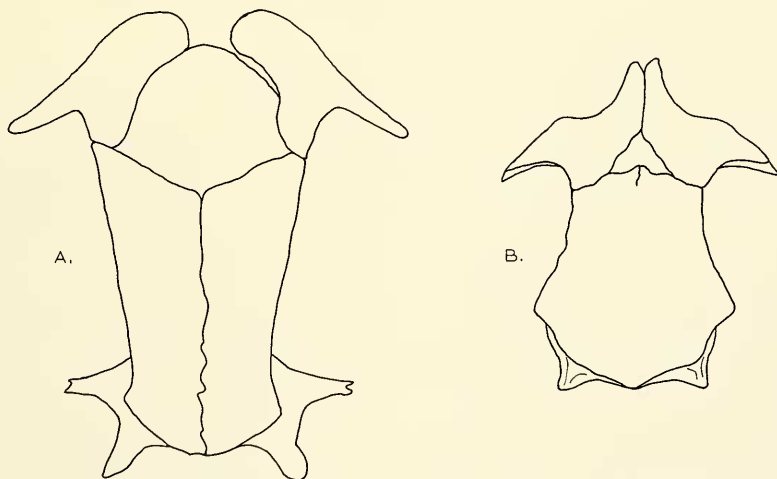
Figure 23. Skull roof of (A) *Megophrys lateralis*, AM 23549; (B) *Pelobates fuscus*, MCZ 1012; both × 3.
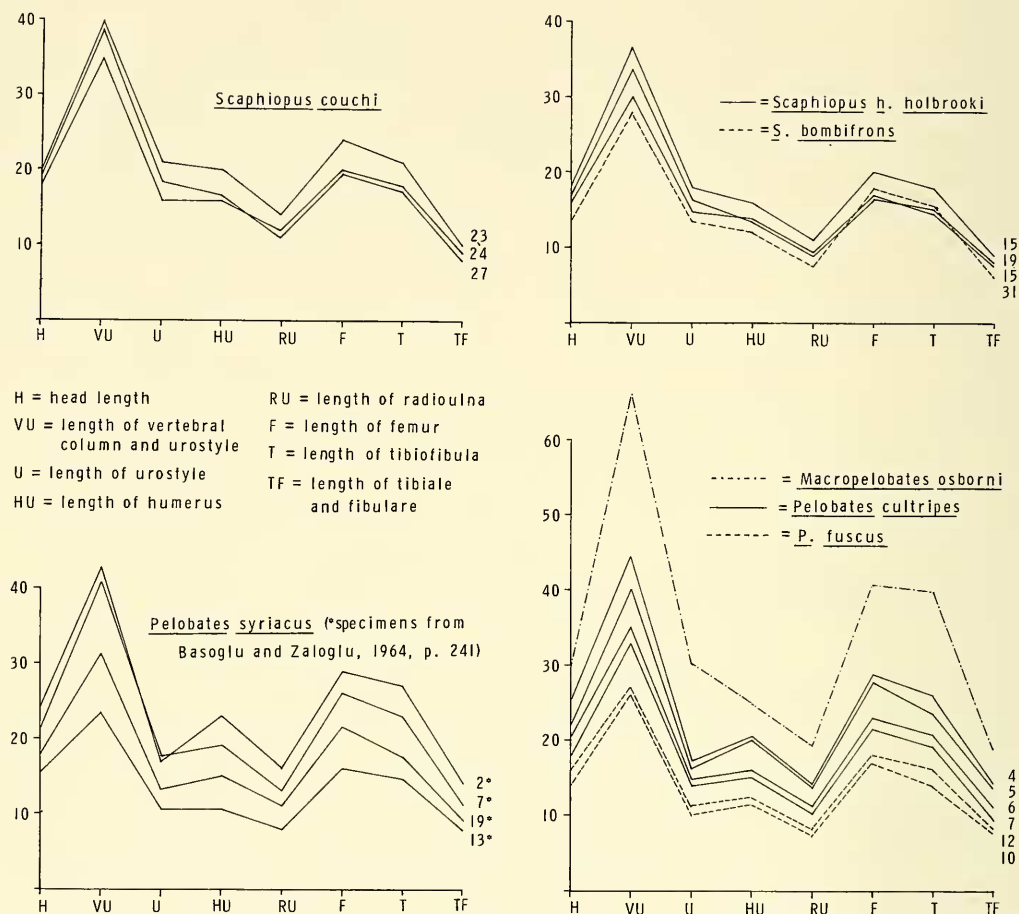
Figure 24. Body proportions of pelobatids. Measurements in millimeters.

pelobatines, the tibiofibula is always a spade, and possession of a well-developed shorter than the femur.

With increasing body size, all pelobatids show allometry in the vertebral column and hind limbs relative to other parts of the skeleton (Figs. 24–25), and the allometric pattern is distinctive for the individual groups. Within the megophryines, the primitive *Leptobrachium* (see Inger, 1966) has head and vertebral proportions as in *Pelobates* rather than as in *Megophrys;* some similarity to *Eopelobates* (especially *E. anthracinus*) occurs as well. So far as my few specimens indicate, the mainland species *M. aceras* shows an *Eopelobates*-like elongation of the tibiofibula whereas the East Indian *M. monticola* and *Leptobrachium hasselti* have a subequal femur and tibiofibula. The Burmese specimen of *M. carinensis* has a tibiofibula slightly shorter than the femur, a proportion reminiscent of pelobatines. Two groups within *Megophrys* seem distinguishable on the basis of the few species and specimens available to me: the one group having relatively short, anteriorly-directed posterior transverse processes, fused urostyles, and body proportions like those of *Eopelobates hinschei;* the other
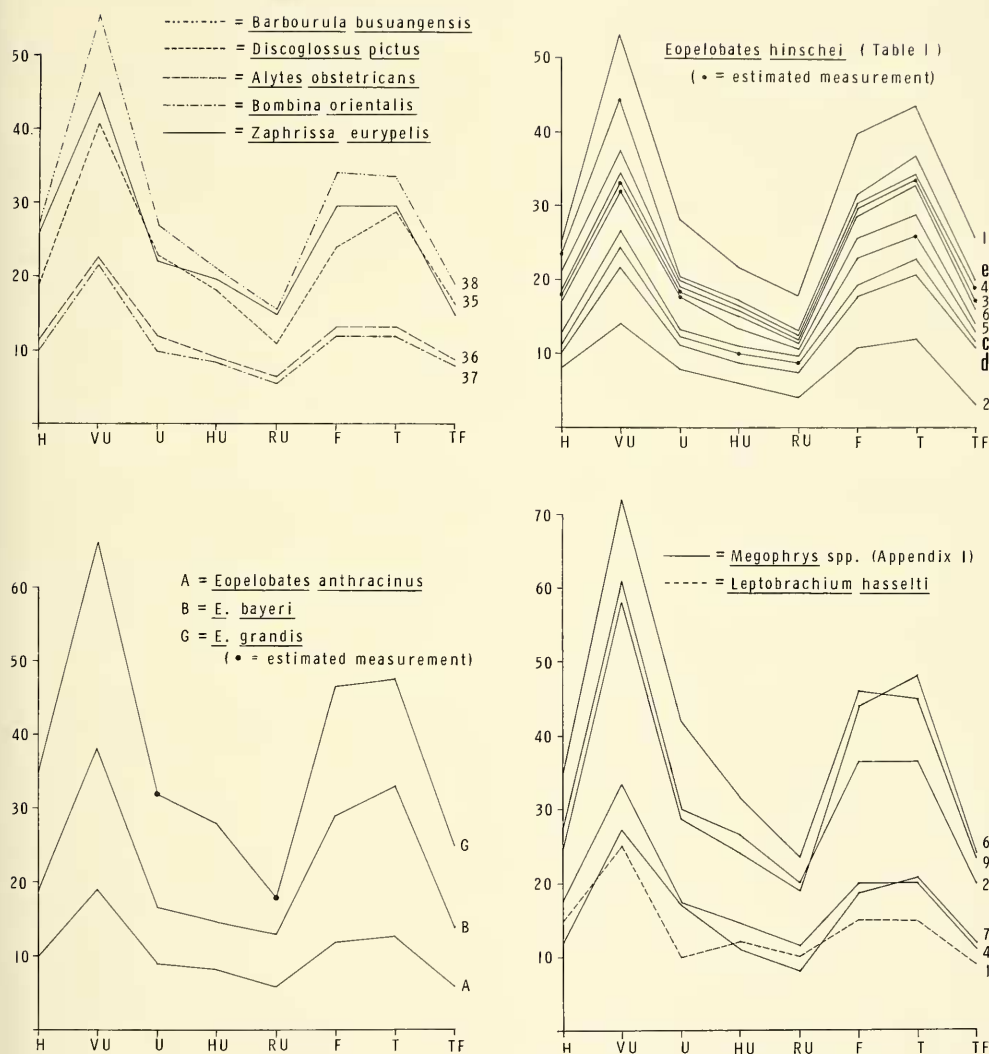
Figure 25. Body proportions of pelobatids and discoglossids. Measurements in millimeters.

group having loose urostyles, elongated, more perpendicular posterior transverse processes, and limb proportions closer to those of the pelobatines. The latter group is less *Eopelobates*-like in the last two features.

Leptobrachium is primitive in having short, anteriorly-directed posterior transverse processes as in *Eopelobates* and (to

lesser degree) as in pelobatines. The first group of *Megophrys* noted above is more like *Leptobrachium* in this regard; the second and more terrestrial group is distant from the latter and approaches the terrestrial pelobatines in limb proportions.

Zweifel (1956, p. 13) emphasized the relationship of *Eopelobates* and *Megophrys* first noted by Špinar (1952, p. 487).

The characters used by Zweifel require some qualification and are discussed *seriatim*:

(1) ". . . only the complete postorbital arch will distinguish [*Eopelobates*] from [*Megophrys*]." As noted above, a squamoso-frontoparietal arch does not exist in *Eopelobates*. In pelobatines this arch is present only in *Pelobates cultripes* (lacking in small individuals), and in most *P. syriacus* (Başoğlu and Zaloğlu, 1964, p. 239). This condition is discussed more fully in the section on anatomical features at the beginning of this paper.

(2) Long transverse processes of the second, third, and fourth vertebrae are present in *Eopelobates* and in most *Megophrys*. In *Eopelobates* their breadth is equivalent to the length of from five to seven vertebrae; the greater the number, the larger the specimen. In *Megophrys* the range is from four to seven vertebrae, again increasing with size. In *Pelobates* this breadth covers only from four to five vertebrae; even the large *P. cultripes* and *Macropelobates* do not exceed this figure. In *Scaphiopus* the range is from four to six vertebrae, and the entire range is encompassed by the *S. couchi* specimens in my sample. This character is therefore not entirely clearcut, but *Eopelobates* and *Megophrys* show the greatest general similarity.

(3) The greatly expanded sacral diapophyses common to *Eopelobates* and some *Megophrys* can be duplicated in *Pelobates cultripes*. The length of the diapophyses in the latter is equivalent to the length of about four or five presacral vertebrae, in *Eopelobates* the range is about four to seven vertebrae, and in no *Megophrys* available to me does it exceed 3.5 vertebrae.

(4) The shape of the bony sternal style is similar and the bone is elongated in both *Eopelobates* and *Megophrys*. However, in *Pelobates cultripes* the shape is close to that of *E. bayeri* and *E. grandis* and is relatively wider throughout its length in

these three species than in *Megophrys* of equal size (Fig. 9).

(5) The free urostyle with transverse processes is similar in some *Megophrys* and some *Eopelobates*, and fusion is variable in both genera. The urostyle of *Pelobates cultripes* is also suturally separate, although partial fusion may have taken place internally. As has been pointed out by many authors (most recently Kluge, 1966), this character is of little value as presently understood. However, some of the intraspecific variation noted in *Megophrys* by various authors was the result of incorrect identification; this character may deserve more careful study.

(6) The great posterior extent of the ischium is similar in both *Megophrys* and *Eopelobates*. Some approach to this condition may be found in *Macropelobates* but the latter more closely resembles *Pelobates cultripes* in this regard (Fig. 26). In this respect the megophryine resemblance is more clear cut.

Thus only 1 and 6 are clear cut resemblances (but to different subfamilies), 2 is perhaps megophryine, 3 and 4 resemble both subfamilies, and 5 is inconclusive. The following characters further emphasize the mosaic of megophryine and pelobatine characters of *Eopelobates*. The *Eopelobates* ethmoid resembles that of the megophryines; in the prootic foramen (known only in *E. guthriei*) and orbitotemporal opening there are resemblances to both subfamilies; in body proportions the variation in pelobatines and *Eopelobates* is encompassed by that found in *Megophrys*. *Eopelobates* (except *E. guthriei*) has a broad, thin, anterior lamina on the scapula that is well developed even in the small *E. anthracinus*. Among pelobatines, only *Pelobates* has such a structure, although it is less well developed.

Intrageneric Classification

From the above it is clear that *Eopelobates* is not a subgenus of *Megophrys* as Zweifel (1956, p. 13) suggested. Although
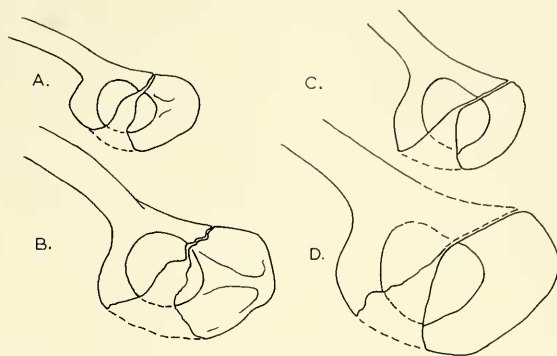
Figure 26.   Pelves in left lateral view. a, Leptobrachium hasselti, MCZ 22626, × 3; b, M. monticola nasuta, MCZ 22640, × 1.8; c, Pelobates cultripes, UMMZ S-2631, × 3; d, Macropelobates osborni, AM 6252, × 1.8. Dashed line indicates restoration.

it is related to the latter genus, it also resembles pelobatines in many features. Examination of the various species of *Eopelobates* might indicate to some workers that several genera rather than one are included. *E. hinschei* and *E. anthracinus*, for example, might be referred to two genera if the other species were unknown. Hecht (1963, p. 23) has already suggested that *E. grandis* is "probably another genus distinct from the European [*E. anthracinus*]," and that at least two types of pelobatids are present in the Geiseltal frog fauna. As far as the latter case is concerned, after examining the Geiseltal collection in 1965 and 1967, I found no reason to recognize species additional to *E. hinschei*, although it is possible that I overlooked another form. *E. grandis* is similar in body proportions to *E. anthracinus*, as is *E. guthriei* in frontoparietal shape; these three species seem to form a short-skulled lineage. *E. bayeri* and *E. hinschei*, on the other hand, are relatively long-skulled forms, at least as far as proportions of nasal and frontoparietal are concerned. These two lineages appear to be linked by the distinctive squamosal shape of *E. hinschei* and *E. guthriei* on the one hand, and of *E. anthracinus* and *E. bayeri* on the other. In addition, *E. grandis*, *E. bayeri*, and *E. hinschei* show similarities of the fronto-parietal border. The rather granular dermal sculpture pattern of *E. grandis* is superficially different from the open, ridged pattern of *E. hinschei*, but these intergrade through the other species.

The list of similarities given at the beginning of this paper indicates that for the present it is best to include all of these species in one genus; I believe that no useful purpose would be served by distinguishing the two lines within *Eopelobates* generically. The situation is somewhat similar to that in the *Scaphiopus-Spea* complex, and the morphological differences are nearly of the same order. Since most recent workers who have dealt with both recent and fossil forms have preferred only subgeneric distinction of *Scaphiopus* and *Spea* (Zweifel, 1956; Kluge, 1966), retention of the fossil species in one genus, *Eopelobates*, makes the internal classification of pelobatids more consistent. I prefer not to apply subgeneric distinctions to the two inferred fossil lineages without better knowledge of the record, however.

Adaptation and Intrafamilial Classification

In the final analysis of *Eopelobates*, it is clear that its position cannot be defined in terms of the archetypal and hierarchial series of stages proposed by Noble (1924, p. 9) and utilized by Parker (1929, p. 280).

Kluge's statements on generic definition (1966, p. 18) are pertinent to this problem. Rather than giving unnecessary emphasis to either a "classical morphotype" or an "adaptive" approach, he shows that both approaches produce similar results when treated in an evolutionary context incorporating the pattern of variation displayed by the organisms. *Eopelobates* or any other fossil must, of course, be defined on observable, hence morphological criteria. Yet when it is compared with living representatives whose adaptive characteristics may be more fully known, its own adaptive features may be assessed more meaningfully.

In this context, it is a frog having a tendency towards elongated limb and body segments, especially those of the distal hind limb. This produces an adaptation, similar to that of many species of *Rana* (e.g. *R. pipiens*), as a semiaquatic, saltatorial animal. It is even more similar in proportions to the living *Discoglossus* (also semiaquatic and saltatorial) than it is to the other discoglossids, *Bombina* and *Alytes*, which are more terrestrial and have more compact, pelobatine proportions (Figs. 24, 25).

The fused dermal skull casque is reminiscent of such fossil discoglossids as *Latonia* and *Zaphrissa* and may have been derived from some common ancestor, although as noted at the beginning of this paper it may be a separately derived condition. The thin anterior lamina on the scapula also occurs in discoglossids, although the scapula is much shorter.

Eopelobates can thus be viewed as a primitive pelobatid, and in the light of the characters discussed above, one not easily relegated to either of the living subfamilies. In an evolutionary approach, subfamilial or other taxonomic boundaries are by definition arbitrary. *Eopelobates* is intermediate between megophryines and pelobatines, and *Macropelobates* connects it with the latter. The Megophryinae are defined by characters not found in fossils

(Beddard, 1907), but should these become known for *Eopelobates*, it is possible that the fossil genus would show an intermediate condition here as well. For the sake of convenience, distinction between the two subfamilies can be maintained by the presence or absence of a spade; in this context *Eopelobates* becomes the most pelobatine member of the Megophryinae; *Macropelobates* the most megophryine of the Pelobatinae.

An alternative position would be to place *Eopelobates* in a monotypic subfamily ancestral to the two Recent subfamilies. I have emphasized the position of *Eopelobates* as intermediate between the two currently recognized groups, yet I have also attempted to show that it is more closely related to the Megophryinae. In part the decision is determined by one's philosophy of classification. I prefer to emphasize the megophryine relationships here, but it is quite possible that more detailed study of the Czechoslovakian specimens will show that there is sufficient justification for separate subfamily status of *Eopelobates* (Špinar, in litt., 1969).

THE PELOBATINAE

The most primitive known spadefoot toad is *Macropelobates osborni* Noble (1924), from the Hsanda Gol Formation of Mongolia. Originally believed to be of late Oligocene age, the associated fauna is now thought to be at about the boundary between early and middle Oligocene (Mellett, 1968).

Recent preparation of the unique specimen of *Macropelobates* has shown features that further confirm its primitive pelobatine position, and which must be discussed before considering spadefoot evolution as a whole.

Macropelobates osborni Noble 1924

The skull of *Macropelobates* is somewhat dislocated, but it is possible to restore its general proportions with fair certainty. The
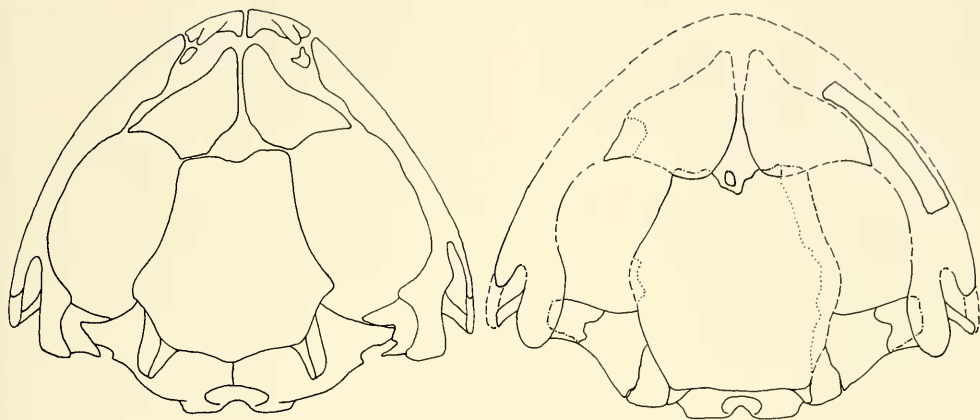
Figure 27.   Left, skull roof of cleared and stained *Pelabates syriacus balcanicus,* MCZ 50690, × 3; right, restoration of skull roof of *Macrapelabates asbarni,* AM 6252, × 1.8.   Dashed line = restoration; dotted line = broken bone edge; dotted and dashed line = bone barder covered by other bone in life.

breadth across the back of the skull can be determined since the dorsal part of the squamosal is present and the otoccipital is complete laterally. Most of the ethmoid is present, and, by comparison with all other pelobatids, it seems clear that the skull did not exceed 30–32 mm in length. The suggested proportions are compared with (e.g.) *Pelobates syriacus* in Figure 27.

The dorsal surface of the skull is flattened or slightly concave, as in most megophryines, including *Eopelobates.* The rounded tympanic process of the squamosal is pelobatine rather than *Eopelobates*-like. There is a posterior process on the maxilla (the latter bone is forced into the left orbit and was called the ethmoid by Noble) indicating the probable presence of a quadratojugal and hence of a complete maxillary arcade. The smooth and essentially complete borders of the frontoparietal and the posterior part of the squamosal indicate that no postorbital bone bridge was present between these two bones. As in *Pelobates cultripes, P. fuscus,* and small *P. syriacus,* there is an opening on the midline between frontoparietals and nasals, and, as is common in *P. cultripes,* a small separate nubbin of dermal ossification is present. The nasals are miss-

ing but the facet for the posterior border is present on the left side of the ethmoid, and a faint impression occurs medially on the ethmoid. The medial part of the posterior border of the otoccipital is expanded posteriorly as in *Pelobates,* and the tip of the prootic part of the otoccipital is narrow, also as in *Pelobates.* In general shape and lack of a thickened and projecting anterior process, the ethmoid is like *P. cultripes* and *P. syriacus* rather than *P. fuscus* or *Scaphiopus* (Figs. 5, 7). A moderately developed turbinal fold is present as in *Pelobates,* and in anterior view the ethmoid is similar to that of *P. cultripes* (Fig. 3).

The tarsus is completely pelobatine (Fig. 28). The tibiale and fibulare are about the same length as the radius, as in *P. cultripes, P. fuscus, Leptobrachium,* and some primitive *Megophrys,* rather than being significantly longer as in *Eopelobates* or shorter as in some *Scaphiopus* and *P. syriacus.* The tibiale is strongly expanded distally as in all pelobatines. A sickle-shaped, enlarged prehallux (spade) is present and closely bound to a large proximal element or pretarsal. Lateral to this is a large centrale 1, followed by distal tarsal 1. The well-ossified tarsus of megophryines includes a large fused distal tarsal 2 + 3, even in small
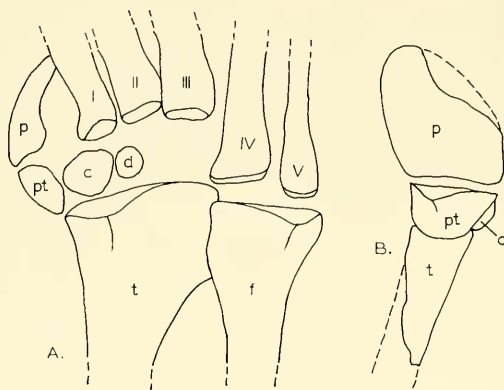
Figure 28. *Macropelobates osborni*, AM 6252; *a*, plantar view of right ankle; *b*, lateral view of spade; × 3. I–V = metatarsals; c = centrale 1; d = distal tarsal 1; f = fibulare; p = prehallux; pt = pretarsal; t = tibiale.

individuals. In pelobatines the latter bone does not ossify, but the other bones occur in all species. In *Scaphiopus* (*Spea*) and *S.* (*Scaphiopus*) *couchi* the pretarsal and prehallux fuse.

The tibiofibula is shorter than the femur as in all pelobatines.

The length from the dorsal border of the acetabulum to the anterior tip of the ilium approximately equals that of the femur. This is greater ilial elongation than is common in pelobatines but such proportions do occur in large *Pelobates cultripes*. The ischial projection posteriorly is more as in *Pelobates* than in *Eopelobates* or *Megophrys* (Fig. 26).

The sacral diapophyses are expanded to about the length of 4.5 presacral vertebrae as in *Pelobates*. The forward inclination of the transverse processes of the posterior vertebrae is not quite so extreme as in *Pelobates* and is more like that of most *Megophrys* and *Eopelobates*.

The urostyle is elongate, exceeding the length of the sacral diapophyses and about equalling or exceeding the length of the skull. In this feature it is in general agreement with that of megophryines and, to a lesser degree, *Scaphiopus*; it is unlike that of *Pelobates*, contrary to the statement of Zweifel (1956, p. 12).

The flatness of the skull surface, the lesser inclination of posterior transverse processes, and the elongated urostyle are the only features that distinguish *Macropelobates* from *Pelobates*. These features are similar to those of *Eopelobates* and some *Megophrys*, and are probably primitive for the Pelobatidae. The other features of the skeleton relate *Macropelobates* closely to *Pelobates* (especially *P. cultripes*) and to the new *Scaphiopus* described below; this serves to clarify and expand Noble's concept of this genus as differing only slightly from the modern forms. Zweifel (1956) and Parker (1929) have cited a similarity of proportions of *Eopelobates*, *Megophrys*, and *Macropelobates*. As Figures 24, 25, and 29 show, the latter is clearly on the pelobatine growth curve. Only the elongated urostyle can be cited as a megophryine proportional feature.

Macropelobates seems to represent an early member of the pelobatines, in diagnostic ways characteristic of that group, but possessing a few features relating the spadefoots more closely to the megophryines. It is closest, however, to *Pelobates*, especially *P. cultripes*, and can only be separated from it by the megophryine primitive characters noted above and by the absence of the enlarged dermal covering of the squamosal and the squamosal-frontoparietal bridge.

Pelobates

The fact that *Macropelobates* seems to have its closest relationships to *P. cultripes*[1] probably indicates the primitive position of the latter species. Gislén (1936) has already considered *P. cultripes* primitive on the basis of size, parasphenoid teeth, and frontoparietal-squamosal connection. The first two characteristics, however, are of little value. The frontoparietal-

[1] Here, as elsewhere in this discussion unless otherwise stated, the conditions of the very closely related *Pelobates varaldii* (Pasteur and Bons, 1959) are as in *P. cultripes*.
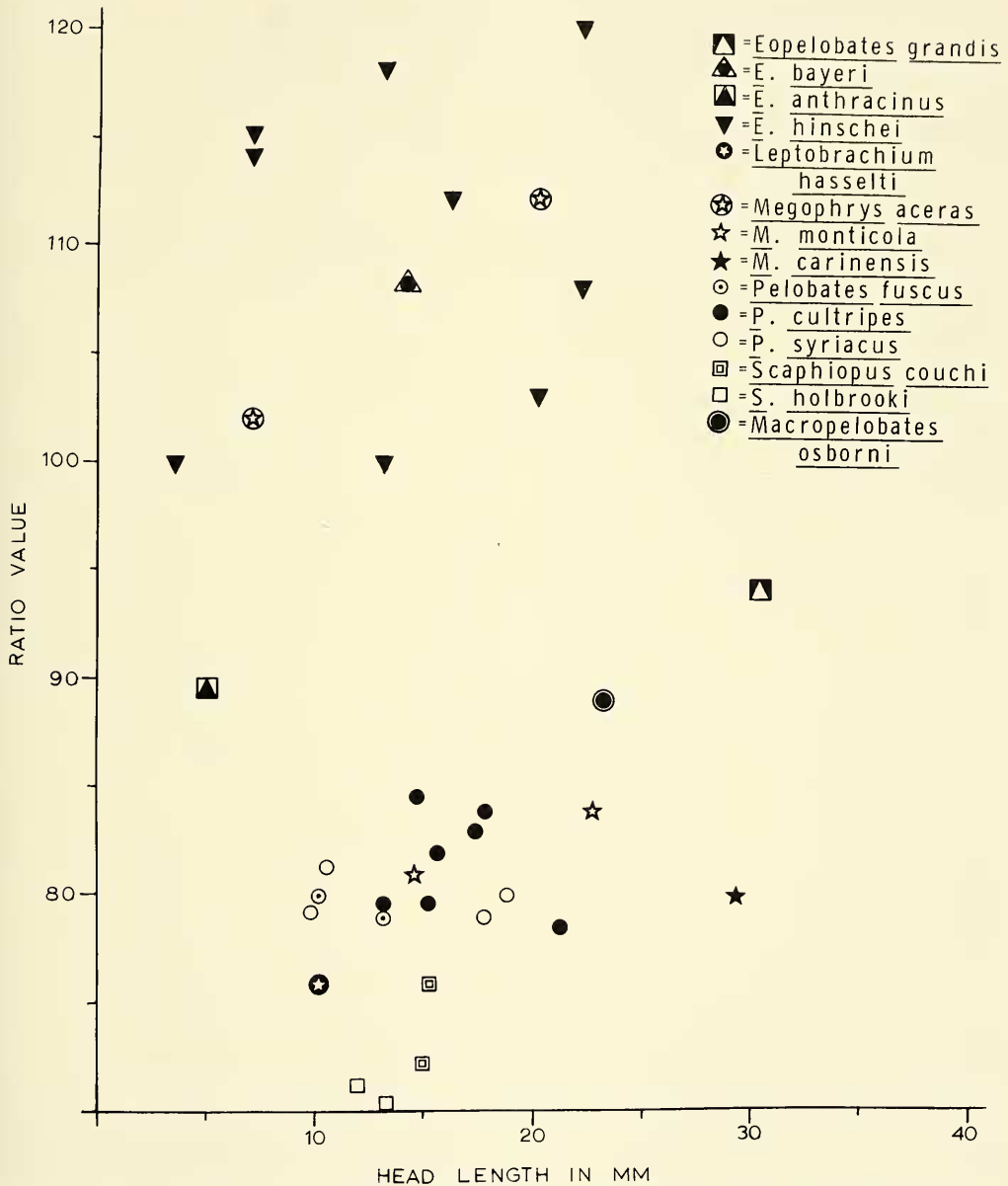
Figure 29. Ratio of tibiofibula-femur length to head-body (skull-urostyle) length plotted against head length for various pelobatids.

squamosal connection was shown to be a secondary condition in the discussion of anatomical features at the beginning of this paper.

Pelobates syriacus is most closely related to *P. cultripes.* Both *P. cultripes* and *P. syriacus,* as well as the primitive *Scaphiopus holbrooki* and *S. skinneri* described below, have an ethmoid with little ossification of the anterior process, but *P. fuscus*

has developed a complex anterior process similar to that of the specialized *Scaphiopus couchi*. While *P. fuscus* has an unusual prootic foramen (Kluge, 1966, p. 13; Fig. 16, this paper), *P. cultripes* and *P. syriacus* have one or more open, megophryine type as in Figure 16b. *P. syriacus* has a tibiale and fibulare shorter than the radius, a condition advanced over that of *S. holbrooki* and more like that of the specialized *S. couchi*. Thus both *P. syriacus* and *P. fuscus* appear to be advanced over *P. cultripes*, although in different ways and to different degree; *P. fuscus* is the more specialized of the two former species. Zweifel (1956) has suggested that *P. fuscus* is most like *S. holbrooki*, but as the description (see below) of the new Oligocene *Scaphiopus* material shows, *Macropelobates* is probably phyletically closer to the ancestral spadefoot than is the relatively specialized *P. fuscus*.

Miopelobates robustus (Bolkay, 1913)

Pelobates robustus Bolkay (1913), from the Lower Pliocene of Hungary, was described on the basis of maxillae, premaxillae, angular, thyroid process of hyoid, and ilium, all fragmentary. Bolkay noted that the maxillae were not completely covered with osteoderms, the anterior part being relatively smooth and separated from the sculptured posterior area by a "bifurcated furrow" (1913, p. 219, pl. 11, fig. 1).

Wettstein-Westersheimb (1955) described *Miopelobates zapfei* on the basis of frontoparietals, nasals, maxillae, sacra, urostyles, and vertebrae from the Middle Miocene fissures near Neudorf, Czechoslovakia. The material is dissociated although some of it, designated "Typen" by Wettstein (1955, p. 812), may be from the same individual. The paired frontoparietals are in contrast with those of *Pelobates*, *Macropelobates*, and *Eopelobates bayeri*. The nasals are compact and *Scaphiopus*-like in appearance, although there was apparently a dorsal exposure of the ethmoid. The maxillae differ from those of *Eopelobates*

bayeri in lacking a lobed squamosal process and sinuous posterior border. The expanded squamosals are most like those of *Pelobates cultripes*. The relatively straight borders of the sacral diapophyses are more as in *Pelobates* than in *Eopelobates*.

The peculiar smooth anterior portion of the maxillae, the suborbital sculptured area, and the bifurcated furrow (for facial blood vessels and nerves) separating these two areas are clearly visible on Wettstein's specimens (1955, pl. 2, fig. 3a) and there seems little doubt that Wettstein's species *zapfei* is a synonym of *robustus*. The very *Pelobates*-like ilium that Bolkay associated with *P. robustus* suggests that *Miopelobates* is a pelobatine. This is supported by the configuration of the squamosals, the sacra, and the nasals as noted above. Because of the paired frontoparietals and the peculiar ossification pattern, this species is retained in Wettstein's genus *Miopelobates*. Kluge (1966, p. 16) allied *Miopelobates* with the Megophryinae, but for the above reasons I believe it to have been a spadefoot. It may have been a somewhat aberrant offshoot from the ancestral *Pelobates* type, and may be near *P. cultripes* as indicated by the expanded squamosals.

Młynarski (1961) has cited a possible occurrence of *Miopelobates* from the Lower Pliocene of Poland; this is very likely in view of its now recognized occurrence in the Lower Pliocene of Hungary.

Scaphiopus

Since both Zweifel (1956) and Kluge (1966) recently discussed the evolution of the North American spadefoots, discussion here will be limited to the pertinence of the new Oligocene *Scaphiopus* described below to their scheme of spadefoot diversification.

Scaphiopus skinneri, n. sp.

Type: FAM 42920, complete skull and vertebral column, left scapula, right coracoid, left? thyroid ossification.

Referred specimens: FAM 42921, one left and one right frontoparietal, both fragmentary, and a partial vertebral column with adherent tibiofibular fragment.

Etymology: Patronym for Mr. Morris Skinner, Frick Laboratory, American Museum of Natural History, who collected the type specimen in 1950.

Locality: Leo Fitterer Ranch, Sect. 7, T 137 N, R 97 W, 13 miles South, 8 miles west of Dickenson, Stark County, North Dakota.

Horizon: First banded zone, 15 feet above base of channel deposits, Unit no. 6A (Skinner, 1951, p. 53).

Age: Middle Oligocene, Orellan (European equivalent = Helvetian).

Preservation: The skull, vertebral column and girdle elements are associated and in almost natural position. The skull has been separated from the vertebral column for study. The skull is well preserved on the right side, but on the left, part of the posterior region of the squamosal and the left frontoparietal are lost. The left otoccipital had been dislocated at the time of burial (probably when the squamosal and frontoparietal were lost) but has been prepared free and replaced in its natural position. Otherwise the skull is undistorted and uncrushed. The atlas and the neural arch of the fourth vertebra are lost, as are the tips of the transverse processes of all vertebrae.

Description: In posterior view the skull roof appears essentially flat but is slightly depressed medially. The occipital canal opens just medial to the prominent paroccipital process. The foramen magnum is a flattened oval; its apex is directed dorsally. The occipital region is well preserved, although the left frontoparietal, left stapes, and lateral edges of the otoccipital are missing. The otoccipitals extend laterad to form the border of the fenestra ovalis. Dorsally they articulate with the frontoparietal and ventrally with the parasphenoid, which is excluded from the fenestra ovalis. The foramen for the ninth and tenth cranial nerves opens prominently just lateral to the large, rounded occipital condyles. The paroccipital process has a prominent boss on its lateral tip, just lateral to the frontoparietal and the occipital canal. The prootic is notched laterally, and forms the medial border of the foramen for the maxillomandibular branch of the trigeminal nerve. The stapes is just posterior and dorsal to this foramen, and has a forked head fitting into the anterodorsal part of the fenestra ovalis. A large opercular space remains, but if a calcified operculum was present, it has been lost. Since such delicate structures as tooth crowns, septomaxillae, and stapes remain, it is likely not to have been present. The prominent descending suspensorium is formed by the pterygoid medially, and the squamosal laterally, which clasp between them the well-developed quadrate.

Dorsally the premaxillae are unsculptured; the right bone is well preserved but the nasal process of the left is missing. The nasals are prominently sculptured and complete except for their pointed anterior processes above the nasal openings. They articulate on the midline where they form a slight depression, and also laterally with the maxillae. There is no open groove or unsculptured area in the nasomaxillary suture. The frontoparietals are also sculptured and have a prominent postorbital projection (broken except on FAM no. 42921a, Fig. 30). Anteriorly they articulate with the nasals but leave a small trapezoidal area of the ethmoid uncovered on the midline. Posteriorly their borders are rounded, curving into the postorbital projection. A tiny, pointed, and unsculptured process of the frontoparietal extends onto the paroccipital process. Maxillae and squamosals are also completely covered by dermal sculpture; the latter articulate firmly with the former but there is no connection or process of squamosal to or toward the frontoparietals. The tympanic process of the squamosal is prominent and rounded, and a broad prootic process covers the tip of the otoccipital. The latter
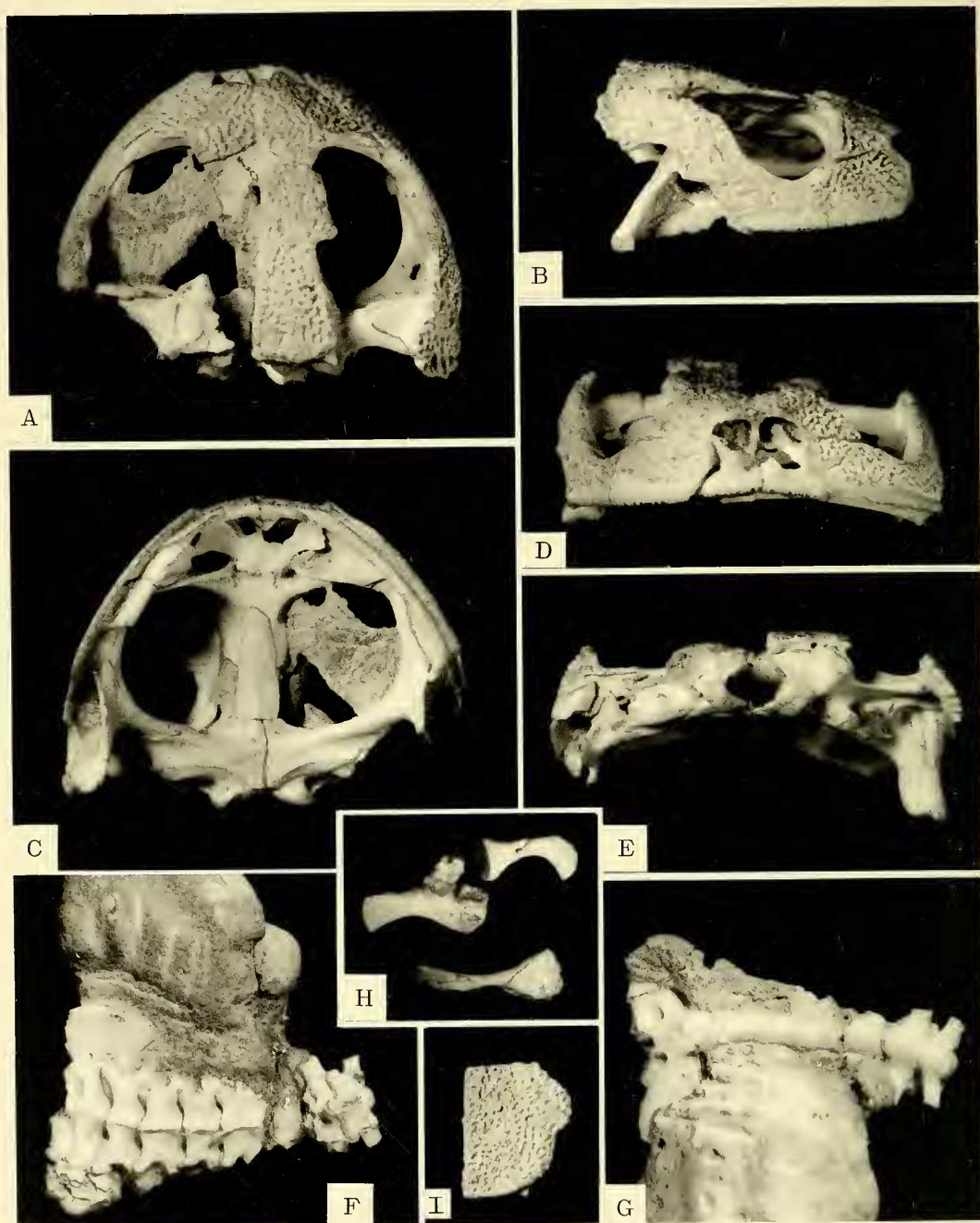
Figure 30. *Scaphiopus skinneri*, n. sp. *A–E*, dorsal, right lateral, ventral, anterior, and occipital views of skull; *F–G*, vertebral column, dorsal and ventral views; *H*, scapula, coracoid, and thyroid process ossification; FAM 42920, ✕ 2. *I*, right frontoparietal, anterior end broken, FAM 42921a; ✕ 2.

bone is exposed to its tip on its posterior end.

Laterally the maxillae are deep and sculptured over all their surface except for a narrow band immediately dorsal to the teeth. The latter are pedicellate, and most of the narrow, spatulate crowns are preserved. The rounded tympanic process of the squamosal extends almost to the occipital condyles posteriorly and is notched ventrally for the tympanic membrane. No quadratojugal is present, although there is, on the lateral surface of the quadrate, a tiny projection that may represent its fused remnant.

In palatal view the vomers have strong processes anterior to the choanae, there are small tooth patches medially, the bones do not meet on the midline, and slim lateral processes to the palatines almost reach the pterygoids. The palatines are completely fused to the maxillae. The ethmoid has strong lateral processes, and well-developed concavities behind the vomers indicate a prominent "turbinal" fold. The anterior tip of the ethmoid is broken away. The pterygoids have a long suture with the maxillae and end in small unossified spaces separating them from the vomers.

The parasphenoid wings clasp the pterygoids laterally; anteriorly the cultriform process lies smoothly on the ethmoid without developing a channel, and posteriorly there are well-defined crests for nuchal and retractor bulbi muscles, and for the eustachian tubes.

The prootic foramen is elongated and open anteriorly; its dorsal and ventral borders are approximately parallel. The oculomotor and optic foramina are not outlined in bone.

The mandibles are broken away posteriorly. Anteriorly the symphysial (mentomeckelian) bones are present, separated from the prearticulars by unossified spaces and clasped by the dentaries.

In anterior view the premaxillae are well preserved but loosely attached. On the right, the ascending process contacts the small septomaxilla. The anterior process of the ethmoid is broken away but was apparently not thickened; a well-defined capsular process with a prominent turbinal fold is visible.

The atlas is missing, as is the neural arch of the fourth vertebra. The vertebrae are procoelous, and, posteriorly, the ninth (sacral) vertebra has well-defined, hatchet-shaped diapophyses. The main postsacral foramina are relatively small, and there appears to have been a smaller second pair as well as considerable webbing (about as in Zweifel, 1956, fig. 19g). The urostyle is broken off but the narrowness of the remaining portion and the presence of two pairs of postsacral foramina indicate without much question that it was fused with the sacrum.

The scapula, coracoid, and ossified thyroid cartilage are all robust but display no unusual characteristics. The disarticulated vertebral column (FAM 42921c) is similar to that of the type.

Discussion: Scaphiopus skinneri, in possessing the following characters, is clearly referable to the subgenus *Scaphiopus*: (1) presence of squamoso-maxillary contact, (2) widely emarginate prootic foramen, (3) absence of frontoparietal fontanelle, (4) extensive dermal skull, (5) probable absence of calcified operculum, (6) presence of pterygoid process of maxilla, (7) presence of palatine, (8) large size. These characters are as given by Kluge (1966, p. 19) except that the condition of the operculum (his character no. 6) is reversed in his table for the two subgenera, although given correctly in the text (1966, p. 10).

In general skull proportions, *Scaphiopus skinneri* is similar to the most primitive living species, S. *holbrooki*. It has a broader skull when compared with length of presacral column: 1/2 skull breadth = 5.5 presacrals as opposed to 4.5 presacrals in a random sample of S. (*Scaphiopus*) at hand, although this relationship may be the result of large size of the fossil. It resembles S.

holbrooki in orbitotemporal opening, although its orbit is not relatively as large (see Fig. 15d, e). As shown by the referred frontoparietals, the postorbital projection is rounded and relatively far forward as in S. *holbrooki.* However, the tympanic process of the squamosal is longer, the posterior extent of dermal bone on squamosal and frontoparietal is greater than in any modern pelobatine, and the skull as a whole is slightly more flattened than in S. *hammondi.* In these characters it resembles *Eopelobates, Macropelobates,* and *Pelobates cultripes.* The tendency in other species of *Scaphiopus* and in *Pelobates* is to develop a more domed skull, although that of *P. cultripes* is flatter than it is in any other living pelobatine. The persistence dorsally of a small area of ethmoid not covered by dermal bone is also a character reminiscent of *Eopelobates, Pelobates fuscus,* and *P. cultripes.* Usually in all *Scaphiopus* (*Scaphiopus*) and in most *P. syriacus,* the dermal covering of the frontoparietals fills this space.

The vertebral column is not unusual except that the second vertebra has the condyle of the atlas fused to it and is hence bicondylar. This fusion is irregular, however, and does not appear to be the usual condition, although it was certainly functional in this individual. A variety of articulations have been noted in pelobatids; Boulenger (1908) found both opisthocoely and procoely in *Megophrys,* and Griffiths (1963) found free intervertebral discs in an adult *Megophrys major* as did Noble (1926). My observations are in accord with theirs, and in addition, I have found free intervertebral discs in a large, cleared and stained adult *Pelobates syriacus* (MCZ 50690). Thus, no significance should be attached to the bicondylar fossil vertebra; all the other vertebrae are procoelous. The length (expansion) of sacral diapophyses in this specimen is equal to the length of nearly three presacral vertebrae, and I have found this to be the case in all individuals in my sample of *Scaphiopus*

(*Scaphiopus*), contrary to the statements of Kluge (1966, p. 17) and Zweifel (1956, Table 1).

The girdle elements and thyroid cartilage ossification resemble those of Recent S. (*Scaphiopus*) and are in about the same size proportion to the skull.

Scaphiopus skinneri is a primitive *Scaphiopus* as shown by the generally more depressed skull, relatively small orbit, flat skull roof, large rounded tympanic process of the squamosal, low squamosal angle (50°; Griffiths, 1963, fig. 2, p. 248 and see section on this character-state at beginning of this paper), posterior extent of dermal bones on frontoparietal, and dorsally exposed ethmoid. Yet, as noted above, it possesses all of the characteristics of the subgenus *Scaphiopus.* In orbitotemporal proportions, degree of expansion of the anterior process of the ethmoid, and short quadrate process of the squamosal, it resembles the most primitive living *Scaphiopus,* S. *holbrooki.*

It is also similar to *Macropelobates* in the large, rounded tympanic process of the squamosal and the shape of the posterior part of the frontoparietal. These are probably primitive pelobatine characters.

Eopelobates guthriei resembles *Scaphiopus* in having a relatively short skull, strongly concave posterior border of the prootic part of the otoccipital, long narrow prootic foramen, and relatively great posterior extent of nasals. It is perhaps the closest to the spadefoot line of any known megophryine. Possibly the two groups had their common ancestor in the Paleocene or perhaps even in the Cretaceous. The fact that the well-defined *Scaphiopus skinneri* occurs in the early Oligocene indicates that the spadefoot line is at least as old as Eocene, and perhaps older; S. *skinneri* also occurs in the early Oligocene of Saskatchewan; this material is being described by Dr. J. Alan Holman.[1] As

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[1] Holman, 1969. Quart. Jour. Florida Acad. Sci. **31**:273–289; received after this paper went to press.

with the living *S. holbrooki, S. skinneri* and probably all primitive *Scaphiopus* were associated with deciduous forests and an essentially humid warm-temperate or subtropical climate (in the sense of Dorf, 1959). The development of the *Spea* complex was probably correlated with the semiarid open woodland scrub and grasslands that were beginning to develop in midcontinental North America by the middle and late Oligocene (Dorf, 1959, p. 189). This is essentially the picture already set forth by Zweifel (1956, p. 41) and supported by Kluge (1966, p. 21).

SPECIES REMOVED FROM THE PELOBATIDAE

Zaphrissa eurypelis Cope 1866, described from the Middle Oligocene lignite beds of Rott, near Bonn, Germany, is usually considered a discoglossid (Friant, 1960). Kuhn (1938, p. 20) synonymized it with *Pelobates* on the basis that Wolterstorff (1929, p. 931) believed it to be "identisch mit *Pelobates decheni* Tr.," but later (Kuhn, 1962) replaced it in the Discoglossidae. Friant (1960) suggested that it might be a juvenile of *Latonia,* a giant discoglossid from the Miocene deposits at Oeningen. The type specimen of *Zaphrissa* was recently rediscovered (Baird, 1970). It has ribs, opisthocoelous vertebrae, a relatively large atlas, a very short scapula, and a double condyle on the urostyle. These characters in combination indicate that the specimen is discoglossid. It has a well-developed dermal skull casque rather like that of *Pelobates cultripes.* The frontoparietal fenestra cited by Cope, and used as an indication of juvenility by Friant (1960), is actually an area where the dermal bone has been broken away before burial, although such a fenestra does occur occasionally even in such a heavily encrusted skull as that of *P. cultripes* (UMMZ S-2630).

I have not seen the material of *Pelobates decheni* noted above, but if Wolterstorff was correct, then the material is incorrectly referred to *Pelobates* and the proper name for this animal would be *Zaphrissa decheni.*

Nevo (1956) gave a preliminary notice of fossil frogs from the early Cretaceous of Israel and stated that the specimens displayed some pelobatid features. Griffiths (1963, pp. 276, 282, 283) later referred to these specimens as pelobatids. A more detailed paper by Nevo (1968) shows these specimens to be members of the Pipidae.

EVOLUTION AND ZOOGEOGRAPHY OF THE PELOBATIDAE

If the late Cretaceous Lance Formation specimens from Wyoming are properly referred to *Eopelobates* (p. 315), then this earliest pelobatid was associated with a humid, subtropical, coastal plain environment in North America (Estes, 1964). The paucity of the Cretaceous record in Europe precludes knowledge of a possibly wider distribution of the group. In any case, the extensive epicontinental seas characteristic of the Northern Hemisphere Cretaceous would probably have hindered or prevented such movement. Holarctic continental connections seem not to have been re-established until the late Paleocene (Russell, 1964), and strong intercontinental faunal similarities persisted until the end of early Eocene time. By this time, *Eopelobates guthriei* was already established in North America and this form may be near the point of divergence of the spadefoot line. *E. guthriei* was associated with a climate essentially like that of the late Cretaceous of Wyoming. Although there is floristic evidence for a period of cooling at the beginning of the Cenozoic (Dorf, 1959), much of the lower vertebrate fauna already established by late Cretaceous time persisted through the Paleocene in Wyoming (Estes, 1962).

Not later than late Paleocene or early Eocene time, *Eopelobates* must have achieved a Holarctic distribution. By mid-

Eocene time, it was well established in Europe in the swamps of the Geiseltal in what was an essentially tropical environment (Krumbiegel, 1959, p. 116). The Geiseltal species, *E. hinschei,* was the most specialized member of the group in that it had developed relatively long posterior limb segments like those of mainland populations of the Recent *Megophrys aceras,* but since the latter is montane the ecology of the two forms must have been quite different. These proportions, in *E. hinschei,* were probably adaptations for an amphibious existence much like that of some species of *Rana,* e.g. *R. pipiens,* which remains on moist banks and uses its long limbs for jumps either for food or to regain the safety of the water.

Although in squamosal shape *Eopelobates hinschei* shows resemblance to *E. guthriei* in North America, it seems to have been the ancestor of a relatively long-headed European line that persisted until at least the middle Miocene.

Eopelobates was also present in North America during the middle Eocene, although the remains are fragmentary. A subtropical climate still persisted in the midcontinental area at this time, but a slight cooling effect has been noted (Dorf, 1959). North American and Eurasian *Eopelobates* must have been pursuing separate evolutionary paths at this time, for faunal interchange was now relatively restricted.

The next record of *Eopelobates* is in the early Oligocene of North America. This animal, *E. grandis* (Zweifel, 1956), is the largest known member of the genus. It resembles *E. guthriei* in having a short, wide frontoparietal, and was almost certainly an autochthonous element.

Early Oligocene also saw the appearance of the first spadefoot toads: *Scaphiopus skinneri* is more primitive than, but is closely related to, the most primitive living species, *S. holbrooki.*

Climatic changes were beginning to take place at this time (early-middle Oligocene);

Eopelobates grandis and *Scaphiopus skinneri* probably lived in a warm-temperate rather than subtropical climate (Dorf, 1959; Clark et al., 1967). The warm temperate flora extended into Alaska (Dorf, 1959) and there was a period of strong faunal interchange (Simpson, 1947). A form close to *Pelobates* was already established in the early Oligocene of Belgium (Hecht and Hoffstetter, 1962). It is possible that spadefoots were derived from *Eopelobates* in the Eocene in North America, or even in the Paleocene. Skull proportions of American *Eopelobates* suggest a closer approach to spadefoot proportions than do those of the long-headed European forms.

E. anthracinus indicates that the short-headed lineage was also present in Europe, however, where it appeared in the middle Oligocene of Germany. It is a relatively short-headed form bearing frontoparietal similarities to the Eocene North American *E. guthriei.* Its squamosals resemble those of the somewhat later *E. bayeri* of Czechoslovakia (cf. Figs. 8, 12, 13, 19, 20), while the body proportions appear similar to those of *E. grandis* (Fig. 24). This may indicate that it was derived from short-headed North American populations that migrated to Europe not later than the early Oligocene, and probably earlier. It might be assumed that its body proportions are the result of its small size, but even small members of *E. hinschei* have body proportions related to those of the large specimens (Fig. 29). On the basis of the short, emarginated frontoparietal, I prefer the first alternative.

At the end of the Oligocene, *Eopelobates bayeri* appears in Central Europe. It persists into the middle Miocene, and is closely related to the Eocene *E. hinschei,* and is also a long-headed form. It probably lived under subtropical conditions in the late Oligocene, which became more warm-temperate in the Miocene (Dorf, 1959). These changing conditions seem to have been related to the disappearance

of *Eopelobates* in Europe by middle Miocene time. *Pelobates*-like fossils are present in France in the late Miocene (Hecht and Hoffstetter, 1962).

The same deteriorating climatic conditions that caused the eventual extinction of *Eopelobates* were favorable to the continued development of the essentially warm-temperate spadefoot line. The first known spadefoot, *Scaphiopus skinneri*, occurs at a latitude transitional at that time between subtropical and warm-temperate conditions (Dorf, 1959). It is probable that this transitional climate was the site of original evolution of the spadefoot type, and that they spread northward from the transition into Temperate regions.

The Eocene of North America was a time of the gradual rise of the midcontinental region. Mountain building activity associated with this rise exposed granitic rocks, whose erosion produced the sandy soils preferred by spadefoots, as well as by other burrowing animals. These soils were (and are) used by spadefoots as a retreat from aridity and because of ease of burrowing. Not only did the mountain building itself cause the developing aridity, but it also produced the soils favoring the fossorial adaptation.

Because the early and middle Oligocene *Scaphiopus skinneri* was already a primitive but well differentiated member of the North American spadefoot line, the Holarctic spread of the spadefoot group must have been *no later* than the late Eocene, when faunal similarities (principally mammalian) indicate that migration was taking place again between Old and New Worlds. The Holarctic radiation was also possible during the early Eocene, and because of the spadefoot resemblances of *Eopelobates guthriei* I favor this alternative (Fig. 31). Since we have no Eocene record of the spadefoots, another possible alternative is that *Scaphiopus* originated in Asia after the early Eocene spread of the ancestral type. In view of the present inadequate

fossil record, the simplest explanation is an autochthonous origin of *Scaphiopus*.

Macropelobates, the primitive *Pelobates*-like spadefoot, appears in Asia by the middle Oligocene. Although it is closer to *Pelobates*, in certain features *Macropelobates* shows some similarities to *Scaphiopus skinneri*, demonstrating some intermediacy between Old and New World forms. The ancestral *Pelobates* populations probably spread westward into Europe no later than early Oligocene, if the material noted by Hecht and Hoffstetter (1962) is indeed *Pelobates* or its ancester. Populations of the genus extended through Northern Europe into the Iberian Peninsula, and evolved into a group ancestral to *P. cultripes* and *P. syriacus*. At the eastern edge of its range, this ancestral group probably formed northern and southern sections on each side of the late Cenozoic Aralocaspian sea-lake (Gislén, 1936; Gignoux, 1955); the modern species had probably evolved by Miocene time. During the Pleistocene, the advancing ice sheets restricted *P. cultripes* and *P. syriacus* to the Iberian Peninsula and Asia Minor, respectively. *P. fuscus*, derived probably from northern populations of *P. syriacus*, remained in Europe wherever the advancing ice sheets permitted, and as Gislén (1936) has already noted, again spread widely over northern Europe during the thermal maximum. Fossils of *Pelobates* have been found in various localities in Europe (see Młynarski, 1961) from at least as far back as the early Pliocene, and other possible occurrences go back to early Oligocene (Hecht and Hoffstetter, 1962). These remains have not been studied carefully by anyone who had an adequate sample of all three Recent species; such a study would be very helpful towards understanding the diversification of the European spadefoots. It seems clear, however, that *P. fuscus* is the most recent and specialized of the three species and that it is not directly related to *Scaphiopus holbrooki*, its ecological
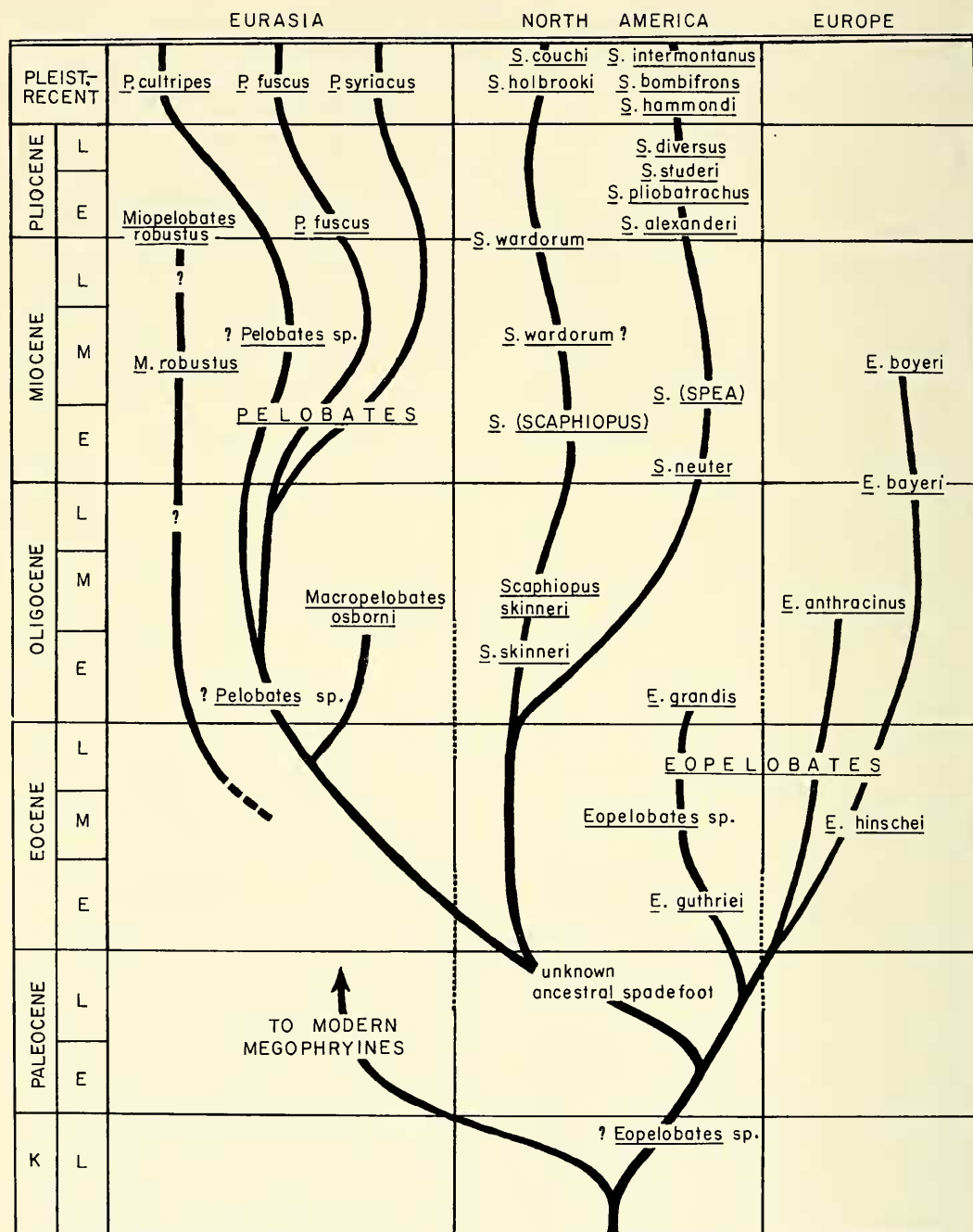
Figure 31.   Temporal, geographical, and inferred phyletic relationships of pelobatids. On the vertical lines separating the continental areas, the times of major faunal exchange (based primarily on mammals; Simpson, 1947) are indicated by broken lines.

equivalent in North America. The findings of this study support Zweifel's contention that *Scaphiopus* and *Pelobates* had a common fossorial ancestor, and that *Macropelobates* is close to that ancestor although too late in time. The patterns of diversification within *Scaphiopus* suggested by Kluge (1966) and Zweifel (1956) are consistent with the known fossils.

The position of the modern megophryines is not directly clarified by this study. It is a diverse group and seems to include animals spanning the range of body proportions found in other pelobatids. Because of the peculiar nature of their dermal ossification, their primitive ethmoid, and the similarity of nasal-fronto-parietal relationships to the early Cenozoic long-headed European lineage of *Eopelobates,* I consider them to be of very ancient origin from a common stock with *Eopelobates.* As noted in several places above, the primitive megophryine genus *Leptobrachium* is the closest to *Eopelobates* of any of the modern forms, yet the resemblance is not especially strong. *Eopelobates* may have been in existence in the late Cretaceous, and since all Cenozoic members show pelobatine features not found in modern megophryines, I believe that their common ancestor cannot have been later than the late Cretaceous. *Leptobrachium* and its relatives were probably tropical differentiates of the ancestral pelobatids. Whether or not the resemblance between the long-skulled European *Eopelobates* and the Recent southeast Asian forms implies an origin of pelobatids in the Old World Tropics is conjectural. Zweifel (1956, p. 15) has properly emphasized the caution necessary in making such inferences. Darlington (1957) favors the origin of many groups in the Old World tropics and such an origin has been often assumed by authors dealing more specifically with amphibians (e.g. Noble, 1924). Yet it is perfectly plausible to imagine a common ancestor of megophryines and pelobatines living in relatively high-latitude Holarctic

tropics of the late Mesozoic, and differentiating into tropical *Leptobrachium*-like forms (their descendants remaining still in present day tropics), tropical and subtropical *Eopelobates* (now extinct) and the temperate geographical replacements of the latter, the pelobatines.

In this latter scheme, *Leptobrachium* and its relatives became restricted to the Old World tropics during the early Cenozoic, and subsequently differentiated into a number of island and montane (temperate) forms. *Eopelobates* diversified into mainly subtropical environments, but also extended into tropical areas (*E. hinschei*). With the progressive restriction of high latitude tropical climates during late Cenozoic time, some warm-temperate forms developed into pelobatines, adapting progressively to increasing aridity in both Old and New Worlds by developing a burrowing habitus. They now have a complementary, Holarctic distribution. *Eopelobates* itself was perhaps unable to compete with more successful ecological analogues that were becoming widespread by the Miocene, such as some species of *Rana*, and therefore became extinct.

APPENDIX 1:
LIST OF RECENT COMPARATIVE MATERIAL

Numbers refer to measured specimens, Figures 24, 25. Numbers in parentheses indicate that more than one specimen is listed under a given museum number.

Pelobatidae
Megophryinae

1. *Leptobrachium hasselti,* MCZ 22626, Borneo.
2. *Megophrys monticola nasuta,* MCZ 22640, Borneo.
3. *M. m. nasuta,* MCZ 19756, Sumatra.
4. *M. monticola,* AM 24786, Java.
5. *M. lateralis,* AM 23549, Kuang China.
6. *M. aceras,* AM 23964, Burma.
7. *M. ?aceras,* MCZ 23436, Burma.
8. *M. ?aceras,* MCZ 23437, Burma.
9. *M. carinensis,* AM 23965, Burma.
10. *M. robusta,* MCZ 25735, Thailand.

11. *Scutiger mammatus,* MCZ 17422, Szechuan, China.

Pelobatinae

1. *Pelobates cultripes,* UMMZ S-2629, no data.
2. *P. cultripes,* UMMZ S-2630, no data.
3. *P. cultripes,* UMMZ S-2631, no data.
4. *P. cultripes,* BM 682, Spain.
5. *P. cultripes,* BM 233, Spain.
6. *P. cultripes,* S-002 (Coll. Špinar), France.
7. *P. cultripes,* S-001 (Coll. Špinar), France.
8. *P. varaldii,* MCZ 31970, Morocco.
9. *P. syriacus balcanicus,* MCZ 50690, Romania.
10. *P. fuscus,* MCZ 1012, Italy.
11. *P. fuscus,* MCZ 1013, Italy.
12. *P. fuscus,* MCZ 1353, Italy.
13. *P. fuscus,* MCZ 1012-b, Italy.
14. *P. fuscus,* MCZ 1013-c, Italy.
15. *Scaphiopus h. holbrooki,* MCZ 25577, Massachusetts (2).
16. *S. h. holbrooki,* MCZ 17420–1, Massachusetts (2).
17. *S. h. holbrooki,* MCZ 17418–9, Massachusetts (2).
18. *S. h. holbrooki,* MCZ 28786, Florida.
19. *S. h. holbrooki,* MCZ 58003, Florida.
20. *S. holbrooki hurteri,* AM 44244, Texas.
21. *S. couchi,* AM 14478, Baja California.
22. *S. couchi,* MCZ 64374, Arizona (cleared and stained).
23. *S. couchi,* AM 56284, Arizona.
24. *S. couchi,* AM 57641, Arizona.
25. *S. couchi,* MCZ 3079, Texas.
26. *S. couchi,* MCZ 6710, Texas.
27. *S. couchi,* MCZ 44335, Mexico.
28. *S. couchi,* MCZ 44336, Mexico.
29. *S. intermontanus,* AM 16918, Utah.
30. *S. intermontanus,* AM 16916, Utah.
31. *S. bombifrons,* MCZ 32912, Texas.
32. *S. bombifrons,* MCZ 32913, Texas.
33. *S. bombifrons,* MCZ 32911, Texas.
34. *S. bombifrons,* MCZ 32914, Texas.

Discoglossidae (only specimens used in Fig. 25 listed)

35. *Discoglossus pictus,* MCZ 3196, Corsica.
36. *Alytes obstetricans,* MCZ 904, France.
37. *Bombina orientalis,* MCZ 19722, Korea.
38. *Barbourula busuangensis,* MCZ 25656, Philippines.

Extensive comparison has been made with many specimens of other families of frogs too numerous to mention here. All specimens examined (other than those noted in this appendix from other institutions) are in the collection of the Museum of Comparative Zoology, Harvard University. A list of specimens available in the skeletal collection is available on request from the Curator of Reptiles and Amphibians.

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